Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea)

by

KONRAD FIEDLER

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CONTENTS

ABSTRACT

1.) A quantitative study of the behavioural interactions of 7 European Lycaenidae and 1 Riodinidae species with 2 ant species revealed significant differences between myrmecophilous and myrmecoxenous caterpillars. A functional dorsal nectary organ is decisive for stable ant-associations. Further aspects of the function of the myrmecophilous organs, and the application of the proposed experimental method to comparative surveys are discussed.

2.) The presence of myrmecophilous organs in lycaenid larvae and the shape of their interactions with ants are intimately correlated with the higher classification of the family. The hypothesis of ancestral myrmecophily is rejected, the decisive dorsal nectary organ being an important synapomorphy of the most advanced subfamily Lycaeninae. The characteristic states of myrmecophily are discussed for all higher lycaenid taxa.

3.) Only trophobiotic ant taxa are involved in non-aggressive interactions with lycaenids. Obligatory myrmecophily is mainly confined to ecologically dominant ants that form large, long-lived colonies, and most of such relationships occur in only a limited number of lycaenid lineages, suggesting the occurrence of phyletic preadaptations for obligatory myrmecophily in these particular taxa.

4.) Lycaenidae caterpillars mainly feed on plants of the subclass Rosidae with a distinct predilection of Fabales and Santalales. The hostplant patterns of the higher lycaenid taxa are described. There is little overlap between hostplant patterns of the Lycaenidae and other butterfly families. In contradiction to a recent hypothesis, no close correlation between myrmecophily and the predilection of Fabales or Santalales was found, with roughly 50 % of the myrmecophiles utilizing different foodplants. Neither obligate nor facultative myrmecophiles consistently have a wider hostplant range than myrmecoxenous species, indicating that myrmecophily has only exceptionally influenced the hostplant relationships of lycaenid caterpillars.

5.) The geographic distribution of myrmecophily is intimately correlated with the distribution of the higher lycaenid taxa. Gross patterns of lycaenid distribution point towards an important role of plate tectonics in the separation of the major lineages. The lycaenid faunas of 8 regions are systematically described, and the proportions of ant-associated species are estimated. A clear north-south disparity in the proportion or degree of myrmecophily is not discernible.

6.) Some hypotheses concerning the evolution of myrmecophily in relation to the phylogeny of the Lycaenidae are proposed. Ant-associations have evolved in parallel in 2 lineages (Miletinae and Lycaeninae). In particular, specializations in, and reductions of, myrmecophily are discussed.

7.) An Appendix summarizes data on hostplants and myrmecophily of more than 1000 Lycaenidae species.

INTRODUCTION

Lycaenid myrmecophily: the general framework

The insect order Lepidoptera comprises 150,000—200,000 described species of which only 13,000—15,000 constitute the well-known butterflies (Papilionoidea; Shields 1989a). The Papilionoidea are divided into five probably monophyletic units that usually are given family rank (Papilionidae, Pieridae, Lycaenidae, Riodinidae, and Nymphalidae). Although often treated as a subfamily of the Lycaenidae, recent research on the mainly neotropical Riodinidae supports the distinction of these 2 taxa (Harvey 1987).

In any case the Nymphalidae and Lycaenidae *s. str.* together contain more than 75 % of the whole species diversity of butterflies and this poses the intriguing question as to what selective conditions have led to this predominance. Starting from their common *Bauplan*, the c. 6,500 nymphalid species show a huge diversification in both morphology and biology. This results in a considerable number of monophyletic subunits that can be characterized by their distinctive morphology and/or host-plant preferences (Ackery 1988).

The phylogenetic relationships among the nymphalid groups are not yet resolved and several of these subunits are still treated as distinct families on a merely typological basis. Generally, the evolutionary strategy of the Nymphalidae can be viewed as adaptive radiation into distinct lineages.

In contrast, the Lycaenidae with about 4,400 species (Bridges 1988), are decidedly more homogeneous. The currently recognized 4 subfamilies (Scott & Wright 1990, this study) have rarely been treated as distinct families (see Stempffer 1967 and Eliot 1973 for historical reviews), and the vast majority of species belongs to a single subfamily, the Lycaeninae.

Thus, the adaptive radiation of the Lycaenidae is largely a phenomenon inside one lineage. Several authors (e.g. Malicky 1969b, Atsatt 1981a, Pierce 1984) have suggested that one factor could have played an important role in this evolutionary process: the interactions of numerous Lycaenidae with ants, termed myrmecophily.

Ants are the leading evertebrate predators of arthropods (Hölldobler & Wilson 1990), and they exert a significant selective pressure on lepidopterous larvae in particular (e.g. Tilman 1978, Laine & Niemelä 1980, Warrington & Whittaker 1985, Jones 1987, Whalen & Mackay 1988, Gösswald 1989, Ito & Higashi 1991).

A number of defensive strategies of caterpillars apply, at least in part, to the avoidance of fatal ant attacks. Among these are defensive regurgitations (Common & Bellas 1977, Eisner et al. 1980, Leather & Brotherton 1987, Peterson et al. 1987) or defensive secretions (e.g. Eisner et al. 1970, 1972, Honda 1983a, b), a dense coating with hairs (Ayre & Hitchon 1968, Weseloh 1989), or the construction of protective silk-webs (Ito & Higashi 1991).

A totally different strategy is to coexist with ants in a non-aggressive way. Such coexistence can be seen as myrmecophily in the widest sense, and DeVries (1991) has recently emphasized that ignorance, i.e. indifferent coexistence of predatory ants with caterpillars, is an important step in the evolution of truly myrmecophilous interactions (see also Atsatt 1981a).

Caterpillars are usually rather slowly moving insects with a soft cuticle and are thus almost a prototype of ant prey. Nevertheless, myrmecophily is amazingly widespread within the Lepidoptera, but unfortunately most published reports refer to rather anecdotal observations, and only very few cases of Lepidopteran myrmecophily, outside the Lycaenidae and Riodinidae, are yet sufficiently well understood.

The larvae of several species in various moth families (Tineidae, Psychidae, Cyclotornidae, Batrachedridae, Pyralidae, Noctuidae, Arctiidae; see Hinton 1951, Hölldobler & Wilson 1990 and Tab.1 for further references) are known to live among ants or inside ant nests. There are commensales or refuse-feeders (*Myrmecozela, Atticonviva* [Tineidae], *Pachypodistes* [Pyralidae]), scavengers (e.g. *Iphierga* and *Ardiosteres* [Psychidae], *Epizeuxis* [Noctuidae]), or predators of ant-brood (*Hypophryctoides* [Tineidae], *Batrachedra* [Batrachedridae], *Cyclotorna* [Cyclotornidae]; *Wurthia* and *Niphopyralis* [Pyralidae]). In *Cyclotorna* the relationship to its host-ant genus *Iridomyrmex* is even more intimate: second instar larvae are actively adopted by these ants that also imbibe the larval excretions. Larvae of the Palaearctic noctuid *Conistra (Dasycampa) rubiginea* often enter nests of the ant *Lasius fuliginosus* for pupation, but the details of this relationship remain unknown. Caterpillars of the Oriental tortricid genus *Semutophila* produce anal exsudates containing carbohydrates, and these excretions induce truly trophobiotic associations with ants.

Non-aggressive ant-caterpillar interactions sometimes occur when ants visit lepidopterous larvae while feeding and imbibe the sap flow caused by the caterpillars' feeding activities. Such associations have been reported from several *Ethmia* species (Oecophoridae), the noctuid genus *Othreis*, the pierid genus *Eurema*, and from some Lycaenidae (*Curetis regula*: DeVries 1984; *Lycaena dispar*: Elfferich, pers. comm.). Caterpillars of the Oriental noctuid genus *Homodes* live among weaver ants (*Oecophylla smaragdina*), apparently without being attacked and mimicking the host ants with the help of peculiar epidermal appendages (Kalshoven 1961, Common 1990, Fiedler, pers. observations). Ford (1945) reported that some Pieridae caterpillars are visited by ants that lick up secretions from glandular hairs. However, these secretions are thought to be primarily defensive, at least in the Palaearctic *Gonepteryx rhamni* (Wasserthal, pers. comm.).

A very unusual observation was reported by Ebner (1905): Caterpillars of the saturniid moth *Saturnia pyri* were visited by small red ants (possibly *Myrmica* sp.?) that licked up the defensive secretions from the caterpillars' scoli. A recent investigation of the related *Saturnia (Eudia) pavonia* revealed that these secretions contain proteins, polypeptides and several aromatic compounds (Deml & Dettner 1990). A summary of these caterpillar-ant associations outside the Riodinidae and Lycaenidae is given in Tab.1.

Tab.1: Ant-associations of Lepidoptera caterpillars other than Riodinidae and Lycaenidae.

Family/ Species	Interaction with ants	References
Tineidae:		
Myrmecozela spp.	feeding on nest material and as scavengers in *Formica* nests	Hinton 1951, Emmet 1979
Hypophryctoides dolichoderella	predator of ant pupae in nests of *Hypoclinea* and *Anoplolepis*	Roepke 1925
Atticonviva spp.	feeding on plant material in *Atta* and *Acromyrmex* nests	Hölldobler & Wilson 1990
Psychidae:		
Iphierga spp. *Ardiosteres* spp.	scavengers in nests of *Iridomyrmex*	Dodd 1912, Common 1990
Batrachedridae:		
Batrachedra myrmecophila	predator of ant brood in nests of *Polyrhachis dives*	Hinton 1951
Oecophoridae:		
Ethmia spp.	ants (*Lasius, Formica, Myrmica*) visit feeding places to imbibe sapflow	Thomann 1908
Cyclotornidae:		
Cyclotorna spp.	first instars ectoparasitic on Jassidae, Psyllidae, Cicadellidae, later instars predatory in *Iridomyrmex* nests	Dodd 1912, Common 1990
Saturniidae:		
Saturnia pyri	red ants (*Myrmica* sp.?) lick up defensive secretions from scoli	Ebner 1905
Lasiocampidae:		
Macrothylacia rubi	3rd instar larva found under stone with large *Lasius* nest, ignored	Fiedler, own observation
Tortricidae:		
Semutophila saccharopa	ants (7 genera) feed on anal exsudates (trophobiosis)	Maschwitz et al. 1986
Pyralidae:		
Pachypodistes goeldii	feeds on nest carton of *Hypoclinea gibbosoanalis*	Hagmann 1907
Wurthia spp.	predators of ant brood in *Oecophylla* and *Polyrhachis* nests	Roepke 1916, Kemner 1925

Family/ Species	Interaction with ants	References
Niphopyralis chionensis	scavenger in ant nests	Common 1990
Stenachroia myrmecophila	found in *Crematogaster* galleries	Hölldobler & Wilson 1990
Arctiidae:		
Crambidia casta	larvae feed on lichen in and near *Formica* nests, pupate in the nests	Ayre 1958
Noctuidae:		
Epizeuxis americalis	scavenger in *Formica* nests	Smith 1941
Conistra rubiginea	pupates in nests of *Lasius fuliginosus*	Hinton 1951, Maschwitz, pers. comm.
Homodes spp.	live as mimics among *Oecophylla* ants, relationship unknown	Kalshoven 1961, Common 1990
Othreis fullonia	ants (*Dolichoderus*) visit feeding places, imbibe sapflow	Leefmans 1933
Eublemma albifasciata	larvae receive ant regurgitations and feed on eggs in *Oecophylla* nests	Dejean 1991
Pieridae:		
Catopsilia florella	ants visit feeding places and imbibe sapflow	Leefmans 1933
Pieris spp., *Anthocharis cardamines*, *Leptidea sinapis*	ants lick up secretions from glandular hairs	Ford 1945, Hinton 1951

A number of further cases of caterpillar myrmecophily will undoubtedly be detected in the course of future research, especially in families such as Tineidae, Pyralidae and Noctuidae, and in tropical regions. However, most of these cases of ant-associations refer to single exceptions in species-rich families where the majority of larvae do never associate with ants.

In addition, no peculiar myrmecophilous organs (e.g. glands) are hitherto known from them. Instead, these caterpillars largely rely, as far as is known today, upon protective silk-webs (*Myrmecozela, Semutophila*), cases built from plant or nest material (Psychidae, Pyralidae) etc. Chemical camouflage via acquired host odour may well be involved as in one myrmecophilous scarabaeid beetle (VanderMeer & Wojcik 1982). In addition, chemical mimicry with the help of cuticular hydrocarbons as exhibited by myrmecophilous syrphid larvae of the genus *Microdon* may also occur (Howard et al. 1990).

In the butterfly families Riodinidae and Lycaenidae, however, numerous species associate with ants. Harvey (1987) estimated the number of myrmecophilous Riodinidae to about 250 species, and in the Lycaenidae more than 3,000 species may be associated with ants. The ant-associated larvae of both families possess a number of highly specialized myrmecophilous organs, and these organs as well as some further adaptations are the basis for their myrmecophilous interactions which by far exceed other cases of lepidopteran myrmecophily in terms of both diversity and complexity.

In this monograph I shall only discuss the myrmecophily of the Lycaenidae s. str. with main focus on caterpillar-ant interactions. The pupae of many Lycaenidae as well as the adults of some species, too, associate with ants, and both phenomena will be considered where appropriate.

The myrmecophily of lycaenid pupae has been discussed in detail by Fiedler (1988a). Bourquin (1953), Ross (1964a, 1966), Callaghan (1977, 1982, 1986a, b, 1989), Schremmer (1978), Horvitz & Schemske (1984), Horvitz et al. (1987), Harvey (1987), and DeVries (1988, 1990a, b, 1991) gave important accounts of the larval biology and myrmecophilous relationships of the family Riodinidae.

Non-aggressive associations of caterpillars with ants attracted the attention of the early naturalists in the second half of the 18th century. By the middle of the 19th century, several European lycaenids were already known to have myrmecophilous caterpillars, and in 1867 Guenée first described the dorsal nectary organ. In the following decades a growing body of evidence was built up concerning life-histories of lycaenids including numerous tropical species.

However, most of these reports were purely descriptive or even anecdotal, and this continues to a considerable degree until today. The first detailed morphological and histological investigations of the myrmecophilous organs were carried out by Newcomer (1912) and Ehrhardt (1914), and by the middle of this century the scattered information had been compiled and thoroughly reviewed twice (Warnecke 1932/33, Hinton 1951).

It was Malicky who laid the basis for our current knowledge of lycaenid-ant interactions in his outstanding extensive compilatory and experimental studies (1969a, b, 1970a, b). During the last decade the myrmecophilous relationships of the Lycaenidae have again received enhanced attention. Pierce and her coworkers focused on the behavioural ecology of, and selective forces acting in, caterpillar-ant interactions (Pierce & Mead 1981, Pierce 1983, 1989, Pierce & Elgar 1985, Pierce & Eastseal 1986, Pierce & Young 1986, Pierce et al. 1987 & 1990, Smiley et al. 1988, Elgar, Pierce 1988).

Furthermore, Pierce (1984, 1985, 1987) and Pierce & Elgar (1985) proposed some hypotheses concerning the evolution and biogeography of lycaenid myrmecophily that were readily taken up in general textbooks on behavioural ecology and evolution.

Henning (1983a, b) studied the chemical communication between caterpillars and ants, and Fiedler & Maschwitz (1988a, b, 1989a, b) analysed certain behavioural interactions. Cottrell (1984) gave a detailed modern review, and the description of life histories was

continued by a number of authors. As a basis for the main topics of this study, I give a comprehensive summary of the current state of the knowledge about myrmecophily of the Lycaenidae in the following two chapters.

Morphology and function of the myrmecophilous organs of lycaenid caterpillars

The adaptations of lycaenid caterpillars towards myrmecophily can roughly be divided into two categories: "passive" protective characters and "active" exocrine glands. The most important passive preadaptation is the unusually thick and tough cuticle of most lycaenid larvae. As has been demonstrated by Malicky (1969b), the cuticle of lycaenid caterpillars is 5—20 times thicker than that of other lepidopteran caterpillars of comparable size.

In addition, most lycaenid larvae have a peculiar *gestalt* that has often been compared with that of woodlice ("onisciform"): their dorsum is weakly rounded, while the flat venter adheres tightly to the substrate.

Furthermore, most lycaenid larvae can retract their head completely under their prothoracic shield. Thus, the most vulnerable organs (nervous system) are well protected against possible ant-attacks, and the shape of their body together with the toughness of their cuticle allow most larvae to withstand occasional hostile reactions of the ants (Malicky 1969b, 1970a, b; but see Samson & O'Brien 1981).

Other preadaptations are found in the larval behaviour. Usually lycaenid caterpillars move very slowly, and they normally lack the thrashing reflex (Malicky 1969b) that is exhibited by many lepidopterous caterpillars when disturbed (Cornell et al. 1987). Since fast movements and thrashing often cause ants to attack, these behavioural peculiarities are important prerequisites for more advanced myrmecophilous interactions.

By far most important for the maintenance of ant-associations are the myrmecophilous organs of lycaenid caterpillars. Three types of such organs are sufficiently well known, although information on the chemical composition of their secretions is still extremely fragmentary.

The first type are the **pore cupola organs (PCOs**; the terminology of ant organs follows Cottrell 1984 throughout). The PCOs are small glandular structures that are derived from hairs, with the hair shaft transformed into a sieve-plate with numerous minute pores of 0.1—0.2 μm diameter. PCOs occur in both lycaenid larvae and pupae and have been observed in all but one of the species investigated so far (e.g. Malicky 1969b, Ballmer & Pratt 1988).

However, morphology and distribution of the PCOs differ markedly between the subgroups of the Lycaenidae, Miletinae and Curetinae bearing particularly aberrant types (DeVries et al. 1986, Kitching 1987, own unpublished observations). PCOs are present from the first instar on, but generally their number increases with every moult, mature larvae possessing most of them (Malicky 1969b, own observations).

Furthermore, the majority of lycaenid caterpillars have concentrations of PCOs around the spiracles and (if present) around the dorsal nectary organ (see below). Highly myrmecophilous caterpillars seem to bear more PCOs equipped with greater pores (Fiedler, unpublished), but these observations need confirmation based on a larger sample of species.

Sometimes the pores are so minute that they can hardly be detected on SEM photographs. Malicky (1969b, 1970a), based on classical light microscopy, termed such organs lenticles, but since even lenticles of non-myrmecophilous hesperiid larvae have turned out to possess pores when studied with sufficient resolution (Franzl et al. 1984), this distinction is of limited value.

Only one lycaenid species definitely lacks PCOs: *Liphyra brassolis* larvae live as brood predators inside the nests of the extremely aggressive weaver ant, *Oecophylla smaragdina*, where they are protected against attacks by an unusually thickened, carapax-like cuticle (Cottrell 1987, Ballmer & Pratt 1988). Obviously this species has lost the PCOs in favour of an alternative defensive strategy.

The presence of PCOs in the rather large Palaeotropical subfamily Poritiinae requires confirmation using electron microscopy, but the illustrations of Clark & Dickson (1971) indicate that lenticle-like structures are present. All other lycaenid and riodinid larvae examined so far possess PCOs at least around the spiracles.

In 1951, Hinton suspected the PCOs to be the source of substances attractive to ants. This has then been established in considerable detail by Malicky (1969b, 1970a) who demonstrated that the PCOs cause intensive antennation behaviour in ants attending lycaenid larvae.

He also distinguished between two types of antennal reaction of the ants towards lycaenid caterpillars: "groping" (stroking with low frequency and intensity), and "palpation" (intensive and high-frequent antennal stimulation). The latter was typically observed at dense clusters of PCOs or at the DNO, while the former is an ubiquitous exploratory behaviour of many ants to assure the nature of newly discovered objects.

Malicky further proved the glandular nature of the PCOs for a number of species and concluded, based on extensive histological and behavioural observations, that the PCOs play the most important role in mediating lycaenid myrmecophily. No myrmecophilous larvae had at that time ever been found without PCOs, while a number of species with no further myrmecophilous organs present apparently released the same behaviour in attendant ants as those lycaenid larvae with more complex myrmecophilous organs.

Malicky's view has subsequently been adopted by a number of authors (e.g. Henning 1983a, b, Kitching & Luke 1985), but was recently questioned by Fiedler & Maschwitz (1989a, 1990; see below).

Although the important role of the PCOs in the interactions between lycaenid larvae and ants is now well established, the chemical composition of their secretions remains practically unknown. Pierce (1983) found amino acids in extracts obtained by washing pupae of the North American polyommatine species *Glaucopsyche lygdamus*, and the

amounts of amino acids detected in the extracts were highly correlated with the attractiveness of the pupae to ants. But she could not completely rule out the possibility that these amino acids originated from other pupal structures (e.g. dendritic hairs, see below). Furthermore, since pupae of *G. lygdamus* sometimes have a functional dorsal nectary organ (Downey 1965), the presence of amino acids in the PCO secretions needs confirmation.

It is clear from behavioural observations that the chemical signals released by the PCOs must be rather general in facultatively myrmecophilous lycaenids, because in numerous cases ants from different genera or even subfamilies react to the same lycaenid immatures in a similar way (Malicky 1969b, Fiedler, unpublished). Thus, mimics of ant brood pheromones (as supposed by Malicky 1969b) are unlikely to be involved in these cases, while amino acids, to which ants are generally attracted as food, are indeed likely candidates.

In obligatorily myrmecophilous lycaenids that are associated with specific host ant genera or species, only these specific ants adequately respond to the secretions of lycaenid larvae (Pierce 1989).

At least in the Palaearctic genus *Maculinea*, whose larvae live as parasites in *Myrmica* ant nests, brood pheromone mimics are probably used by the larvae (Elmes et al. 1991a, b), and it is well possible that these substances originate from the extremely numerous PCOs of *Maculinea* caterpillars (Fiedler, unpublished). The chemical nature of these adoption substances is unknown, but cuticular hydrocarbons are possibly involved (see Howard et al. 1990 for a parallel case of syrphid myrmecophily; also Brian 1975).

In the Australian genus *Jalmenus*, different concentration profiles of amino acids in the secretions of the dorsal nectary organ are responsible for the recognition and acceptance of the larvae by their appropriate host ants (Pierce 1989), and this may apply to their PCO secretions as well. Several ants are known to respond differentially to the presence and concentrations of various amino acids (Lanza 1988, Lanza & Krauss 1984).

However, not all lycaenid PCOs are attractive to ants. For example, caterpillars of *Callophrys rubi*, although possessing PCOs, were never palpated in experiments with ant species of two subfamilies (Fiedler 1990d). Similarly the PCOs of some riodinid larvae (including myrmecophilous species) are unattractive to ants (DeVries 1988, Harvey 1989), and Ballmer & Pratt (in press) observed very different reactions of *Formica pilicornis* ants to a number of Californian riodinid and lycaenid caterpillars, ranging from permanent attendance to severe attacks (see also Malicky 1970b).

Since all these species tested have PCOs, differences in the function of these organs apparently do exist. Hence, although the important role of the PCOs is clearly documented in many lycaenids, the chemical composition of their secretions and their related biological functions provide a challenge for further investigation.

The second type of myrmecophilous organs is the **dorsal nectary organ (DNO)**, an epidermal gland located on the dorsum of the seventh abdominal segment. Usually the orifice of the DNO is surrounded by a cluster of PCOs and very often by a field of

specialized setae (club-shaped setae, dendritic hairs etc.: Clark & Dickson 1956, 1971, Kitching & Luke 1985, Fiedler 1988b).

The DNO secretes droplets of a clear fluid when stimulated by ants via antennation. Normally attendant ants vigorously palpate the vicinity of the DNO and eagerly imbibe each droplet (Malicky 1969b). The hairs surrounding the DNO are supposed to be sensory, but this requires experimental confirmation.

Malicky (1969b, 1970a) provided evidence that the DNO itself could be derived from hairs, while Kitching & Luke (1985) presumed that the DNO may have evolved from one of the numerous epidermal pores commonly found on lycaenid caterpillars.

In contrast to the PCOs, a functional DNO is usually not present in the pupal stage, although many pupae still bear a scar of the DNO. The only exception was reported from *Glaucopsyche lygdamus*, where Downey (1965) observed a functional DNO in some pupae that all died later.

The ontogeny of the DNO and the mechanism of its function were described in detail by Malicky (1969b). The DNO is normally present and functional from the third larval instar on. There is, however, some variation. In some species the DNO's appearance is delayed until the fourth stage, in very few species it already starts working in the second instar (Clark & Dickson 1956, 1971).

The chemical composition of the DNO secretions is known from only a couple of species. In the secretions of *Polyommatus hispanus* and *P. icarus*, several carbohydrates (total concentrations 10—15 %), but only traces of amino acids were found (Maschwitz et al. 1975). Pierce (1983, 1989) reported variable amounts of carbohydrates and high concentrations of amino acids from *Glaucopsyche lygdamus* and 3 Australian *Jalmenus* species, while in *J. daemeli* the amino acids are apparently replaced by a characteristic oligopeptide. In the riodinid *Thisbe irenea* the secretions from the analogous tentacle nectary organs likewise contain high concentrations of amino acids (DeVries & Baker 1989).

These limited data and the fact that usually attendant ants imbibe the DNO secretions immediately indicate that these secretions provide a valueable food source for ants. Evidently the nutritive compounds are derived from the caterpillars' food, and recent experimental work has shown that the quality of larval food may affect the ability of the larvae to produce their myrmecophilous secretions (Fiedler 1990c, Baylis & Pierce 1991). However, any speculations about systematic or geographical traits (e.g. Pierce 1987) in the composition of the DNO secretions must await further data from a broader spectrum of species.

The DNO is by no means as ubiquitous in the larvae of the Lycaenidae, as are the PCOs. In fact, it is known only from the subfamily Lycaeninae, and even there it is secondarily missing in a number of species or genera. Accordingly, Kitching & Luke (1985) suggested to term all those species without a DNO **"myrmecoxenous"**, a distinction that turned out to be of considerable value for the discussion of the evolutionary and systematic implications of lycaenid myrmecophily (see below).

Throughout this study only species with a functional DNO are called **myrmecophilous** from a morphological point of view. Interestingly, and in contrast to an often repeated belief (e.g. Malicky 1969b), ant-associations of lycaenid larvae without a functional DNO are rare and mostly occur under special circumstances (e.g. carnivorous species). Myrmecophilous Riodinidae possess a pair of tentacle nectary organs that are functionally comparable, but phylogenetically only analogous to the DNO (Cottrell 1984, DeVries 1988).

A third type of myrmecophilous organs are the eversible **tentacle organs (TOs)**, a pair of epidermal tubes located on the dorsum of the eighth abdominal segment of many lycaenid caterpillars. The TOs are everted when the larvae are stimulated by ants or, in some species, when the caterpillars crawl about or are disturbed.

When the everted TOs are touched, they are withdrawn immediately. Normally the TOs of each side of the body are able to act independently from one another, and often the sequence of eversion and retraction of the TOs is repeated several times, resulting in a conspicuous tentacle performance. On the top of each tentacle there are numerous setae, mostly of a dendritic type. The TOs are everted by means of a locally increased hemolymph pressure mediated by the abdominal dorsoventral musculature of the larvae, and they are withdrawn by a peculiar retractor muscle (Malicky 1969b).

Morphologically there are 2 main types of TOs: the rather small "beacon" type that is widely distributed among the subfamily Lycaeninae, and the larger "whip" type that only occurs in the Aphnaeini (Clark & Dickson 1956, 1971). The TOs of the Curetinae (DeVries et al. 1986, Fiedler & Maschwitz, unpublished) are somewhat similar to the Aphnaeini TOs in size and structure.

The function of the TOs has been the subject of controversy over several decades. Based on behavioural observations several early authors (e.g. Thomann 1901) supposed the TOs to be scent organs influencing the ants' behaviour. Ehrhardt (1914) stated that the dendritic hairs on their top are glandular, based on his observation that these hairs bear very large pyriform cell bodies.

Malicky (1969b, 1970a), however, rejected these findings. He was neither able to detect any glandular structures within the TOs, nor any reaction of the ants towards the eversion of these organs (but see Malicky 1961), and he concluded that the TOs of lycaenid caterpillars were nothing more than rudiments of formerly important organs.

However, a number of authors have reported that attendant ants do respond to the eversion of the TOs with alertness or even alarm behaviour (Elfferich 1963b, 1965, Downey & Allyn 1979, Fiedler & Maschwitz 1988b, 1989b, Munguira & Martin 1988, 1989b, Schurian 1989a, Jutzeler 1989a, Ballmer & Pratt in press). This reaction is usually only observed in a radius of a few mm around the TOs.

Furthermore, not all ant species react to the TOs of a given lycaenid species. With the only exception of *Aricia morronensis* (where the dolichoderine ant genus *Tapinoma* showed the characteristic "excited runs": Munguira & Martin 1988), the ants hitherto observed to respond to the TOs all belong to the subfamily Formicinae.

This group-specificity of the reaction observed, and the short active range of the releasing signal, led to the assumption that the TOs produce volatile secretions (possibly mimics of ant alarm-pheromones) causing the alertness of attendant ants. Alarm-pheromones of ants generally are highly volatile, have a short active range, and often one major component occurs in larger systematic groups of the Formicidae (Hölldobler & Wilson 1990).

Chemical support for this pheromone-mimic hypothesis comes from the study of Henning (1983b) who demonstrated that the TOs of the South African Aphnaeini species *Aloeides dentatis* and the alarm-pheromone of its obligate and specific host ant *Acantholepis capensis* yield very similar gas-chromatographic profiles. In 1977, Claassens & Dickson had already demonstrated that caterpillars of the closely related *Aloeides thyra* alert the same host ant species with their TOs when travelling between their feeding places and the ant nests, wherein the caterpillars rest.

Thus, although the ultrastructure of the TOs and the detailed chemical composition of their presumed volatile secretions remain to be examined more closely, there can be no doubt that at least in a number of lycaenid species the TOs are able to activate specific attendant ants.

TOs are present only in the larvae of the subfamilies Curetinae and Lycaeninae (regarding the genus *Aslauga* [Miletinae] see below), but they are missing in even more species and genera than the DNO. Generally, larvae with TOs also possess a DNO, and there are only very few well-documented examples where the larvae only have the TOs (*Curetis*, some *Aloides* spp.). The reverse situation (bearing a DNO, but without TOs), in contrast, is rather common.

In the caterpillars of Theclini, Eumaeini, and Polyommatini the beacon type TOs usually, but not always appear together with the DNO in the third instar. In some species, their appearance is delayed until the fourth stage, in others they develop already in the second (Clark & Dickson 1956).

In Aphnaeini larvae, in contrast, the whip type TOs are present throughout the whole larval period. In this tribe, the DNO develops in the second or third instar. Some species apparently have no DNO at all (*Phasis*), whereas in others it disappears in the ultimate instar (*Aloeides dentatis*?; Clark & Dickson 1956, 1971).

Besides the three main types of myrmecophilous organs (PCOs, DNO, TOs) further larval and pupal characters may be related with myrmecophily. Ballmer & Pratt (1988 and in press) suggest that dendritic setae secrete ant-attractive substances.

Support for this hypothesis comes from the observation that concentrations of dendritic hairs on lycaenid larvae or pupae receive considerably enhanced attention by ants (e.g. spiracles of the prothoracic and sixth abdominal segment of *Polyommatus* or *Lycaena* pupae: Malicky 1969b, Fiedler 1987a). The only four North American *Lycaena* species, that are regularly ant-attended in the field, possess dendritic setae already as larvae. In other *Lycaena* species such setae are confined to the pupae, if they are present at all (Wright 1983, Fiedler 1988b and unpublished, Ballmer & Pratt in press).

Morphological surveys of numerous lycaenid immatures revealed a large diversity of further specialized setae and epidermal pores whose function is still unknown (e.g. Clark & Dickson 1971, Downey & Allyn 1978, 1979, Wright 1983, Kitching 1983, 1987, Kitching & Luke 1985, DeVries et al. 1986, Baylis & Kitching 1988, Fiedler 1988b, 1990d and unpublished results). Some of these structures might play a role in the interactions with ants, as well.

Recently, DeVries (1990a) detected the production of substrate-borne vibrations in myrmecophilous Riodinidae and Lycaenidae larvae. Riodinids "stridulate" with the help of peculiar organs, the "vibratory papillae". In at least one species, *Thisbe irenea*, such vibrational signals enhance the ant-associations of the larvae (DeVries 1988, 1991).

Substrate- as well as air-borne vibrational signals were also found in larvae of several lycaenids (e.g. European *Maculinea, Polyommatus, Cupido* and *Lycaena* species: DeVries 1990a, Schurian, Fiedler & Tautz, unpublished). The mechanism of sound production by lycaenid caterpillars is still unknown. A connection of larval sound production with myrmecophily needs to be proven, but must be taken into account.

The pupae of many lycaenids and riodinids are likewise able to stridulate with a specialized organ located between two abdominal tergites (Hoegh-Guldberg 1972, Downey & Allyn 1973, 1978, Elfferich 1988). This pupal stridulation, however, is currently interpreted mainly as a defensive device (Hoegh-Guldberg 1972, Downey & Allyn 1978).

Adults of a number of lycaenid species also live in associations with ants, particularly in the subfamily Miletinae. Morphological or biochemical adaptations are suspected to occur, but nothing certain is known. Imaginals of several non-related species that pupate in ant nests bear a dense covering of loose hairy scales at eclosion, which prevent ant-attacks while leaving the host nest (Cottrell 1984, 1987).

Communication between lycaenid caterpillars and ants

Lycaenid caterpillars clearly influence or manipulate the behaviour of ants they encounter. First, instead of being attacked and killed as prey, they suppress ant-aggressiveness and are thus normally vigorously palpated or at least ignored by the ants. Ignorance (DeVries 1991) or appeasement (Maschwitz et al. 1985b) are obviously the premise of more complex interactions.

Any caterpillar that fails to appease or deter the ants encountered has a low chance of survival. The chemical basis of appeasement or ignorance is still weakly understood. It has repeatedly been assumed that the PCOs' secretions are responsible for the suppression of ant-aggressiveness (Maschwitz et al. 1985b, Fiedler & Maschwitz 1989a etc.), and the general presence of the PCOs in lycaenid immatures, in concert with the widespread attractiveness of their secretions to ants, strongly support this view.

If the secretions of the PCOs are really basically amino acids (see above), then the "appeasement" of ants is mediated through nutritive components instead of pheromone

mimics. This seems to apply to the great number of facultatively myrmecophilous lycaenids that unspecifically associate with a wide array of ant species.

Furthermore, as has been discussed by Pierce (1989), amino acids may secondarily well play important roles as communicative substances in ants, and she presented evidence that differential responses of ants towards amino acids (see Lanza & Krauss 1984, Lanza 1988) are used in the specific communication of the Australian lycaenid genus *Jalmenus* with its different specific host ants.

In some obligatorily myrmecophilous lycaenids with specific host ants, the caterpillars are able to release brood-carrying behaviour in their appropriate host ants. In these cases mimics of the recognition substances of ant workers or ant brood are suspected.

In ants, such recognition substances are usually cuticular hydrocarbons (Hölldobler & Wilson 1990), and several myrmecophilous insects indeed possess hydrocarbon profiles similar to that of their hosts. These substances may be passively acquired (Scarabaeidae: VanderMeer & Woijcik 1982) or actively biosynthesized (Syrphidae: Howard et al. 1990).

For lycaenid larvae no exact chemical data exist, but Henning (1983b) demonstrated that epidermal extracts of *Lepidochrysops ignota* caterpillars induced carrying and brood-caring behaviour in the specific host ant, *Camponotus niveosetosus*. The rapid adoption of larvae of *Maculinea alcon* and *M. rebeli* (Elmes et al. 1991a, b), *M. nausithous* (Fiedler 1990b), or *Anthene emolus* (Fiedler & Maschwitz 1989b) suggests that these larvae, as well, actively produce the allomones required, whether through the PCOs or elsewhere in the cuticle.

Furthermore, myrmecophilous lycaenid larvae are able to induce food recruitment in their attendant ants by offering their DNO secretions (Fiedler & Maschwitz 1989a). The alerting of attendant ants with the help of the TOs and the possible vibrational communication of lycaenid larvae have already been mentioned.

Summarizing the available evidence, trophic as well as communicative substances certainly govern the interactions of lycaenid caterpillars with ants, with mechanical stimuli as a potential communicative supplement. The ants usually react with antennal stroking or intensive palpation to these signals, and they regularly harvest the caterpillars' secretions.

The communication mechanisms of adult lycaenids remain obscure. Adult Miletinae and Poritiinae often visit ant-homopteran associations to imbibe honeydew without being attacked. The ants regularly touch the butterflies or even climb their legs and wings (Maschwitz et al. 1985a, 1988).

One African Poritiinae species, *Teratoneura isabellae*, apparently deters ants using a volatile chemical (Farquharson 1922). In a number of obligatorily ant-associated lycaenids, the females oviposit amongst their host-ants with no aggressiveness being observed (Atsatt 1981b, Henning 1983a, Cottrell 1984, Pierce & Elgar 1985, Sands 1986).

In all these cases adult appeasement substances might exist as postulated by Maschwitz et al. (1985a). Ovipositing females of *Anthene emolus* are first attacked by their host ant *Oecophylla smaragdina*, but after oviposition has commenced the ants remain calm, suggesting that the scent of the freshly laid eggs might function as an appeasement substance here (Fiedler & Maschwitz 1989b). In contrast, adults of the same lycaenid just eclosing from the pupa are killed as prey.

In at least one miletine species, *Allotinus unicolor*, the butterflies communicate with the ants in a tactile way using their proboscides (Fiedler & Maschwitz 1989c). The relationships of adult lycaenid butterflies towards ants and related adaptations apparently cover a wide range which needs further investigation until generalizations should be made.

Ecology of lycaenid-ant interactions

Two hypotheses, which are by no means mutually exclusive, have been proposed to explain the ecological role of lycaenid myrmecophily. According to the "defence hypothesis", originally proposed by Lenz (1917) and vigorously supported by Malicky (1969b, 1970a), the only selective advantage of myrmecophily is the ability to survive in habitats where aggressive ants are abundant. Malicky (1969b, 1970a), in particular, stated that attendant ants do not yield any protection against enemies to the caterpillars.

The "mutualism hypothesis", in contrast, implies that ant-associations reduce the mortality risk of caterpillars because attendant ants thrive away at least some parasitoids or predators. This hypothesis, of which Thomann (1901) was one of the earlier representatives, was experimentally proven for two lycaenid species by Pierce & Mead (1981), Pierce & Eastseal (1986), and Pierce et al. (1987). Occasional observations on *Anthene emolus* (Fiedler & Maschwitz 1989b), *Brephidium exilis* (Fernandez Haeger 1988) and others further indicate that attendant ants are able to deter part of a caterpillar's enemies.

The interactions between lycaenid larvae and ants range from indifferent coexistence to close and obligatory associations. Warnecke (1932/33), Hinton (1951) and Henning (1983a) have proposed ecological classifications of the Lycaenidae with regard to their life-histories. Since all these groupings are connected continously with each other, I here only give a short characterization of the main types of interactions. The reader is referred to the cited works for details.

The first group to mention are the myrmecoxenous species, i.e. those without a functional DNO (Kitching & Luke 1985). Such caterpillars are very rarely found in stable associations with ants, and their predominant selective advantage is to escape ant attacks. For myrmecoxenous lycaenids only the "defence hypothesis" holds true. Nevertheless, as has been discussed in detail by Lenz (1917), Malicky (1969b) and Atsatt (1981a), this is a highly significant selective advantage, because myrmecoxenous larvae have access to ecological niches where predatory ants limit or even preclude the existence of many other insects. In such niches fewer competitors and enemies exist, offering the caterpillars an "enemy-free space" (Atsatt 1981a).

The second ecological group within the Lycaenidae are the truly myrmecophilous species. Normally these myrmecophiles possess a DNO (and often TOs) and thus are able to secrete nutritive substances towards the ants. Myrmecophilous larvae are attended by ants, but the degree of myrmecophily is again extremely variable. Some species are only exceptionally ant-attended, presumably since they either produce less attractive secretions or live in habitats where contacts with ants seldom occur. Larvae of other species are, at least in later instars, nearly permanently visited by ants. Even more specialized are those lycaenids that are obligatorily associated with a particular host ant genus or species.

Although experimental evidence is currently available only for the two species studied by Pierce and one riodinid (see above), all such myrmecophilous associations of lycaenid caterpillars possessing a DNO are here basically viewed as mutualistic relationships on the following reasoning.

There are numerous examples that trophobiotic associations of homopterans with ants are mutualistic. Attendant ants gain substantial food resources and, in turn, defend their trophobionts (e.g. Way 1963, Messina 1981, Buckley 1987, 1990, Hanks & Sadof 1990, Olmstead & Wood 1990a). This protective effect may vary with ant species (Bristow 1984, Cushman & Addicott 1989), or with time and population density of the trophobionts ("conditional mutualism": Cushman & Whitham 1989).

A somewhat parallel situation exists in plants with extrafloral nectaries that attract ants; such plants are often protected by attendant ants against herbivores (e.g. Tilman 1978, Schemske 1982, Whalen & Mackay 1988, Rico-Gray & Thien 1989), although some studies failed to demonstrate such a protective effect (e.g. O'Dowd & Catchpole 1983).

Based on this evidence as well as the impressive experimental studies of Pierce and her coworkers on *Glaucopsyche lygdamus* and several *Jalmenus* species, it is feasible to assume that stable lycaenid-ant associations represent, in many cases at least, trophobiotic mutualisms, where the caterpillars receive some protection by the ants and reward the latter with nutritive secretions.

Recent studies have shown that caterpillar secretions may indeed contribute significantly to the nourishment of ant colonies (Pierce et al. 1987, Fiedler & Maschwitz 1988a, 1989b). As with the better known mutualisms between ants and plants or homopterans, the protective effect of such symbioses is never perfect.

Ant-plant mutualisms are exploited by herbivores adapted to the presence of ants (e.g. myrmecophilous lycaenid or riodinid caterpillars: Maschwitz et al. 1984, Horvitz & Schemske 1984, DeVries & Baker 1989, DeVries 1990b), and specialized predators invade ant-tended homopteran aggregations (e.g. lycaenid caterpillars of the subfamily Miletinae: Cottrell 1984, Maschwitz et al. 1985a, 1988, Ackery 1990; beetles and syrphid flies: Pontin 1959).

Thus, one cannot anticipate that the protective effect of attendant ants for myrmecophilous lycaenid caterpillars is significant under all circumstances, and the mere observation that myrmecophilous lycaenid caterpillars suffer from parasitism

does not disprove the mutualism hypothesis. Highly adapted parasitoids and predators as well as the ant species involved, the larval population density, and abiotic factors certainly shape and modify the selective outcome of any such association. Clearly this is a field open to further and more detailed research (e.g. Pierce 1989).

In addition, the balance of costs and benefits of myrmecophilous associations probably covers a wide range. When the selective pressure of parasitoids or predators is rather low, or if the caterpillars have alternative defensive strategies, they may produce few or rather unattractive secretions. Then they still retain the important advantage of not being preyed upon by the ants, while the ants receive little or no reward for their lack of aggressiveness. The other extreme are those lycaenids whose survival is impossible without ants due to heavy predation (e.g. *Jalmenus*: Pierce et al. 1987). Between these extremes lies a continuum of potential mutualistic interactions.

A third ecological category are the "parasitic" lycaenid-ant interactions, which can further be subdivided into two classes. Several lycaenid caterpillars destroy the food resources of ants by feeding upon myrmecophytes (Maschwitz et al. 1984) or trophobionts (Maschwitz et al. 1985a, 1988). Such competetive interactions have been termed "indirect parasitism" by Maschwitz & Fiedler (1988).

The larvae of some other lycaenids live inside ant nests where they prey on ant grubs or receive ant regurgitations (see Cottrell 1984 for review), thereby "parasitizing" on the energy budget of the whole ant colony. Again there is a wide spectrum with regard to the impact of the lycaenid larvae on their host ant colony.

Some "parasitic" caterpillars still pass attractive (and presumably nutritive) secretions to the ants (several Aphnaeini, *Acrodipsas*), others only participate in the social food exchange (*Euliphyra mirifica, Maculinea alcon, M. rebeli*), while a third group significantly decimates the immature stages of their respective host colonies (*Maculinea arion, Liphyra brassolis*).

Whether true commensalism as a fourth ecological category does exist among the Lycaenidae is still unclear. However, the larvae of several African Liptenini have apparently been found exclusively in the close vicinity of specific ant nests (Farquharson 1922, Jackson 1937), and these non-predatory larvae are thought to feed on fungi or debris and might thus be examples of true caterpillar-ant commensalisms.

So, the ecological interactions of lycaenid larvae and ants continously cover the wide range from indifferent coexistence, across facultative or obligatory mutualisms, to more or less severe parasitic (and possibly commensalic) interactions.

Aims of the present study

The fascinating phenomenon of myrmecophily has always attracted the attention of entomologists since the 18th century. The last decade brought considerable progress in the understanding of these interactions. Furthermore, the sociobiological paradigm generally stimulated the investigation and interpretation of mutualistic and parasitic systems.

Pierce and her coworkers, in particular, have proposed a number of far-reaching hypotheses regarding the ecology and evolution of lycaenid-ant interactions, mainly based on their experimental work on *Glaucopsyche* and *Jalmenus*. Other new questions arose from the studies of Fiedler & Maschwitz (1988a, b, 1989a).

The present work pursues a twofold aim. In the next main section I shall describe an experimental method to quantitatively analyse the behavioural interactions between lycaenid larvae and ants, with special reference to the function and importance of the various myrmecophilous organs. In particular, I shall examine the role of the DNO and the PCOs in some European species in order to test the findings of Fiedler & Maschwitz (1988a, 1989a) that the DNO is the critical organ for stable and truly mutualistic associations. The role of the myrmecophilous organs, and the distinction between myrmecophilous and myrmecoxenous species, have been insufficiently evaluated in many studies. This section on the experimental ethology of lycaenid-ant interactions is a complete essay for its own.

In the subsequent chapters I shall critically re-examine some of the evolutionary and ecological hypotheses proposed in the recent literature. In contrast to a purely sociobiological view, this re-examination is based on two fundamentals: a basically systematic approach, and a comprehensive and extensive compilation of as much information as available on lycaenid life-histories.

The third chapter gives a review of the modern systematics of the Lycaenidae and describes the trade-offs with myrmecophily. The existence of any such correlations between phylogeny and the myrmecophilous relationships within the Lycaenidae was hitherto rejected by Pierce & Elgar (1985) and Pierce (1987).

In the fourth chapter the specificity of lycaenid-ant interactions will be discussed, with special reference to the lycaenid taxa showing obligatory myrmecophily.

The fifth chapter summarizes the hostplant relationships of the Lycaenidae under a systematic aspect. In particular, the hypothesis of Pierce (1985) that myrmecophilous caterpillars preferentially feed on nitrogen-fixing hostplants is compared with data for more than 1000 lycaenid species.

In the following chapter I describe and analyse the biogeographical patterns of myrmecophily, and the final chapter is devoted to the proposal of some hypotheses concerning the evolution of lycaenid-ant interactions.

This second and main part of the present monograph is basically a comparative, non-experimental study in evolutionary biology. It is founded on data concerning the larval biology and myrmecophily of nearly 1070 lycaenid species. These records, summarized and arranged in tables in the Appendix, were extracted from more than 300 literature sources and include numerous unpublished observations kindly communicated by colleagues.

In face of the tremendously scattered and steadily expanding entomological literature, the database presented is certainly not exhaustive. A considerable amount of informa-

tion on larval hostplants or ant-associations is certainly still hidden in faunistic or rearing reports, often published in only locally distributed journals.

Furthermore, it was impossible to check all old records by myself, and in these cases I must rely on the excellent reviews by Warnecke (1932/33), Hinton (1951), Malicky (1969b), or Cottrell (1984). Notwithstanding, the tables present the most complete compilation of relevant information concerning the larval biology of the Lycaenidae that has yet been published, and the main conclusions drawn from this database should, despite the still significant gaps in our current knowledge, prove reliable.

On this background of a broad "classical" comparative and systematic survey, the present monograph is intended to provide a complement to the sociobiologically and ecologically reasoned hypotheses, which have so markedly stimulated the recent research on the biology and evolution of the Lycaenidae, but currently tend to dominate the discussion. The final goal is an evolutionary synthesis of these two approaches.

BEHAVIOURAL INTERACTIONS BETWEEN LYCAENID LARVAE AND ANTS: A COMPARATIVE EXPERIMENTAL STUDY

The use of quantitative methods in the investigation of myrmecophily

As pointed out above, presence and function of the myrmecophilous organs of lycaenid caterpillars play essential roles in the outcome of encounters with ants. The experiments of Fiedler & Maschwitz (1988a, b, 1989a) strongly indicate that the morphological distinction between myrmecoxenous caterpillars with only PCOs present, and myrmecophilous larvae possessing an additional DNO (and often a pair of TOs), has a behavioural as well as an ecological correlate.

Larvae with a functional DNO are generally more attractive to ants, and they are able to release food recruitment behaviour in ants, thereby inducing stable associations that may be further enhanced by the use of the TOs or vibrational communication. Hence, such larvae are much more likely to be attended by ants in the field.

This view, however, contradicts the findings of Malicky (1969b). According to him all lycaenid caterpillars are treated by appropriate ants in basically the same way, the large variability observed not being correlated with the presence or absence of the DNO or TOs. Furthermore, Malicky denied differences between caterpillars with or without a DNO regarding ant-associations in the field. To decide this controversy, it is thus necessary to investigate the behavioural interactions between caterpillars and ants in more detail.

In the following I describe a quantitative method for comparing lycaenid-ant interactions. As Malicky's experiments were not intended to yield quantitative data for statistical evaluations, a direct comparison with his results is possible to only a limited degree. The single other quantitative study available is that of Ballmer & Pratt (in press) on Californian lycaenids (see discussion).

Although recruitment experiments proved the existence of one important difference in the behaviour of ants towards myrmecophilous and myrmecoxenous caterpillars (Fiedler & Maschwitz 1989a), such experiments have considerable practical disadvantages:

First, the willingness of ants to perform food recruitment largely depends on the nutritive status of the colony as a whole. It is difficult and time-consuming to assess this status and even more problematic to warrant standardized experimental conditions.

Secondly, the number of ant workers in a colony and the number of ants that engage in foraging may provide a source of great variance. Even using the same ant colony all the time does not rule out such differences.

Thirdly, recruitment trials have to last considerable time; e.g. with the ant *Tetramorium caespitum* an experimental duration of one hour was found to be necessary (Fiedler & Maschwitz 1989a).

Hence, only a limited set of data can be sampled per day. Given the difficulties of breeding lycaenid caterpillars and the often short and unpredictable availability of ap-

propriate instars, I thus decided to develop a more standardized and easily replicable experimental method to allow quantitative comparisons for at least a small range of species.

Material and methods

Larvae of the only European riodinid *Hamearis lucina* L., 1758 and of 7 European lycaenid species were examined. The latter were: 3 myrmecophilous *Polyommatus* species (*coridon* Poda, 1766; *icarus* Rottemburg, 1775; and *escheri* Hübner, 1823), 3 *Lycaena* species without a DNO (*phlaeas* L., 1761; *tityrus* Poda, 1766; and *hippothoe* L., 1761), and *Callophrys rubi* L., 1758 whose larvae possess a DNO, but no TOs. *H. lucina* is myrmecoxenous, too (cf. Malicky 1969a).

This range of species covers three of the five tribes of the Lycaeninae, namely Lycaenini, Eumaeini, and Polyommatini. *H. lucina* belongs to the subfamily Hamearinae. The latter taxon retains a number of plesiomorphic traits and is thus viewed as the most primitive subfamily of the lycaenids' presumed sister-family Riodinidae (Harvey 1987). Unfortunately, no representatives of the tropical subfamilies Curetinae, Miletinae and Poritiinae, and no species of the Lycaeninae tribes Aphnaeini and Theclini were available.

P. icarus, the *Lycaena* species, *C. rubi* (in part), and *H. lucina* were reared from eggs obtained from captive females, while *P. coridon, P. escheri* and *C. rubi* (in part) were collected as 2nd or 3rd instar larvae. The rearing method largely followed Schurian (1989a), modifications for single species were given by Fiedler (1989a, 1990a, d, e).

For experiments only final instar larvae (i.e. 4th instars in all species examined) were used. Two ant species from different subfamilies were employed, viz. *Tetramorium caespitum* (Myrmicinae) and *Lasius flavus* (Formicinae). Colonies of both were kept in earth nests in a greenhouse under nearly ambient conditions and were fed honey-water and cockroaches as needed.

For experiments, 25 (*L. flavus*) or 50 (*T. caespitum*) worker ants were taken from the colonies and put into clear plastic boxes (10 x 10 x 6 cm). A transparent lid prevented the ants from escape. The larger ant number with *T. caespitum* reflects the smaller size and lower activity of this species when compared with *L. flavus*.

Only ants freely foraging in their nest containers were used to ensure that they would readily display trophobiotic behaviour when encountering the caterpillars. The ants then were left undisturbed until they had calmed down for at least 10 min. Subsequently, two mature lycaenid larvae (usually belonging to the same species) were carefully introduced, and the behaviours of the caterpillars and ants were observed for 30 min.

Every 30 s the number of ants actually associated with each caterpillar was recorded, and the visits of ants at the DNO, the DNO secretion rates and eversions of the TOs were counted throughout. An ant was considered as associated with a caterpillar if it was either sitting on the latter, or if it had antennal contact to the larva.

After 30 min the caterpillars were removed, and the ants were left undisturbed for at least 15 min until the next test with two new larvae took place. The same group of ants was never used for more than three successive trials, since after 1—2 h of separation from their nests most ants showed reduced activity or otherwise abnormal behaviour. All experiments were conducted at 22—26 °C with indirect daylight in a southwest-facing room between 10.00 and 18.00 CEST. Every 7.5 min the experimental box was rotated by 90 ° to avoid any bias through possible preferences of ants or caterpillars for the darker or brighter corners.

In several larvae of *Polyommatus coridon* and *P. icarus* the DNO was covered with a cap of glue (UHU schnellfest plus™) in order to investigate whether this exclusion of the DNO resulted in a detectable change of the behaviours of attendant ants. This treatment had no adverse effects on the caterpillars and all pupated and eventually produced sound adults.

The influence of larval hostplants on the myrmecophilous qualities of *P. icarus* caterpillars, as measured in experiments of the same design, has already been reported in detail (Fiedler 1990a, c).

The observational data were used to calculate the following myrmecophily parameters:

1.) Larval attractiveness, **A:** the mean number of ants attending each larva;
2.) Relative variablity of attractiveness, **RV:** the standard deviation of A divided by A (this quotient is usually termed coefficient of variation: Sachs 1978);
3.) Permanence of ant-association, **P:** the number of counts when a larva was attended by at least one ant, divided by the total number of counts (i.e. divided by 30 for 15-min trials).

These parameters as well as the secretion and eversion rates of the DNO or TOs, respectively, were then statistically evaluated using the non-parametric U-test of Mann & Whitney (Caradoc-Davies 1985).

A preliminary survey showed that *L. flavus* (which was the distinctly more active ant species) tended to visit caterpillars most intensively during the first half of the 30-min experiments, while the reverse was true for *T. caespitum*. Thus, in order not to underestimate the attractiveness of the lycaenid larvae, the parameters A, RV and P were calculated separately for the first and second half of each 30-min trial.

For further analyses the first-half values were used with *L. flavus* and the second-half values with *T. caespitum*. A parallel evaluation of the combined data did not yield different results with regard to significance of interspecific differences.

Ballmer & Pratt (in press), for their different approach to measure the permanence of ant-associations, present their percentage data in an arcsine-transformed manner. To facilitate direct comparisons, all figures for P obtained in this study are thus additionally given in the same transformation.

Results

Myrmecophilous species

Polyommatus coridon — Caterpillars of *P. coridon* were always intensively palpated by both ant species and usually received permanent attention. The ants' in-

terest concentrated upon the DNO and the spiracles, and on numerous occasions the ants were observed to nibble at the PCOs, presumably harvesting their secretions. Aggressive behaviours of the ants (biting, stinging, spraying of defensive secretions) were never observed.

The larvae showed no signs of being disturbed by the ants and often walked through the experimental box carrying several ants on their backs. Even when a caterpillar fell off the side-parts of the box, the ants never responded aggressively, but with a short increase in their locomotion activity at most.

The release of DNO secretion droplets was commonly observed, but due to the almost continous presence of ants around the DNO the exact secretion rates could not be established with certainty. Fiedler & Maschwitz (1988a) have reported secretion rates of 15-74 droplets/h (mean 31 droplets/h) when observing *P. coridon* larvae under a stereo microscope.

In the experiments with the ant *L. flavus*, the DNO was on average intensively palpated 20.79 times (S.D. = 5.12) in 15 min. In the same trials, the TOs were everted with a mean rate of 24.13 per 15 min, but with a considerable higher variance (S.D. = 12.69). While in 4 cases more than 40 eversions were observed, 2 larvae used their TOs less than 10 times.

L. flavus worker ants regularly responded to contacts with everted TOs displaying excited runs as described by Elfferich (1965) and Fiedler & Maschwitz (1988b), while ants of the myrmicine species *T. caespitum* did never.

The myrmecophily parameters A, RV and P of *P. coridon* larvae were significantly different from all other lycaenid species tested with *L. flavus* (see Tab.2a). With *T. caespitum* the attractiveness A of *P. coridon* caterpillars was again significantly higher than that of the other lycaenids investigated, while the parameters RV and P were similar to those of the 2 further *Polyommatus* species, but different from the values obtained with the myrmecoxenous larvae (Tab.2b).

During the experiments the caterpillars often produced faecal pellets (usually one per larva and trial). In four out of 24 occasions, 1—3 (maximum 6) ants of the species *L. flavus* intensively chewed and sucked at the fresh pellets for several minutes, but without reducing the ant-association of the larva itself. *T. caespitum* showed no interest in the caterpillar frass.

Exclusion of the DNO (only tested here with the ant *L. flavus*) significantly influenced the behaviour of ants towards the larvae. The attractiveness of the larvae was reduced to less than half the figure of intact caterpillars, while RV increased by about 50 %. The strongest effect was observed at the DNO itself: the DNO region was on average only palpated 2.86 times (S.D. = 2.49) in 15 min, i.e. about 10 % of the figure observed with intact larvae. The cap of glue had no noticeable deterrent effect on the ants; the ants were simply no more attracted to the DNO. The reduction of the permanence of the ant-associations was less distinct, but still highly significant.

The function of the TOs, however, was not significantly affected (mean eversion rate = 20.82, S.D. = 8.43). Clearly, the exclusion of the DNO rendered *P. coridon* caterpillars less attractive to ants with a more fluctuating and less stable ant-association, but they remained ant-attended to a considerable degree (Tab.2a).

Polyommatus icarus — Caterpillars of this species were treated by both ant species in a way similar to that observed with *P. coridon*, but intensive palpation was more markedly restricted to the DNO and to the PCO accumulations at the spiracles. No aggressiveness of the ants was ever observed, and the caterpillars often calmly walked about carrying ants on their backs.

However, the myrmecophily parameters of *P. icarus* caterpillars significantly differed from those of *P. coridon* (all data regarding *P. icarus* refer to larvae reared on herbaceous Fabaceae, see Fiedler 1990a, c). Their attractiveness was only about one third with both ant species, and in the experiments with *L. flavus*, larvae of *P. icarus* had more fluctuating and less permanent ant-associations than *P. coridon* caterpillars (Tab.2a).

Important differences were observed with regard to the function of the myrmecophilous organs. *L. flavus* ants palpated the DNO on average 26.35 times in 30 min, but with a high variance (S.D. = 16.32). This rate, when compared with the 15-min figure of *P. coridon* (20.79), indicates a distinctly lower attractiveness of the DNO in *P. icarus. T. caespitum* ants palpated the DNO of *P. icarus* with a similar mean frequency (28.21 ± 21.85 in 30 min). This same ant species usually attends the DNO of *P. coridon* caterpillars so constantly that it is nearly impossible to count distinct palpation events.

In *P. icarus* larvae DNO secretions were only observed within the last 2 days of the ultimate larval instar, and in trials with *T. caespitum* the actual secretion rate was low and rather unpredictable even then (2.68 ± 2.86 droplets/30 min), yielding an estimated mean rate of 5—6 droplets/h (*P. coridon*: 31 droplets/h).

The frequency of intensive palpation at the DNO was highly significantly correlated with all 3 myrmecophily parameters (experiments with *L. flavus*; Spearman's rank correlation; A: $r_S = 0.60$, RV: $r_S = -0.64$, P: $r_S = 0.66$; $p < 0.001$, $n = 26$), which indicates that the activity of the DNO is the main factor governing the ant-associations of *P. icarus* larvae.

Regarding the activity of the TOs, again important differences were found between *P. icarus* and its congener *P. coridon*. With both ant species tested the eversion rates of the TOs were equally low and highly variable in *P. icarus* (*L. flavus* [30 min]: 5.96 ± 8.01; *T. caespitum* [30 min]: 6.84 ± 8.95). In only 16 out of 90 experiments TO eversion rates of 15—40/30 min were observed, while in 28 trials the caterpillars did not use their TOs at all.

As with *P. coridon*, only the ant species *L. flavus*, but not *T. caespitum* responded to contacts with everted TOs by the typical excited runs, although this reaction was usually less pronounced. Nevertheless, there was a significant correlation between the eversion rate of the TOs and the parameters P (Spearman's rank correlation coefficient r_S =

0.56, $p < 0.002$, $n = 26$) and RV ($r_S = -0.52$, $p < 0.002$), suggesting that the TOs indeed enhance the stability and permanence of larval ant-associations as proposed by Fiedler & Maschwitz (1988b). Larval attractiveness or the frequency of intensive stimulation of the DNO, in contrast, were not significantly correlated with the activity of the TOs.

The caterpillars regularly produced faecal pellets during the experiments. *L. flavus* responded to the fresh frass in 13 of 26 occasions with intensive chewing and sucking. Within 5 min the pellets became thus literally dry and shrimpeled. On at least two occasions the pellets were immediately taken by worker ants from the larval anus. *T. caespitum* showed no interest in the frass. Preliminary tests with the ninhydrine reagent proved the presence of considerable amounts of amino acids in the frass.

P. icarus caterpillars, albeit significantly less myrmecophilous than the congeneric *P. coridon*, received distinct attention by ants and regularly induced rather stable ant-associations. This was no longer the case when their DNO was rendered unfunctional (experiments with *L. flavus*). Covering the DNO with a cap of glue led to a complete breakdown of their ant-association (Tab.2a).

Ants then only sporadically visited the larvae for short times, and intensive palpation was hardly ever observed. The DNO was visited on average only 9.70 times (S.D. = 7.48) in 30 min, and usually the ants soon left it. Attacks did never occur, but the ants took very little interest in the caterpillars.

Unfortunately, in these experiments the TOs were likewise actually excluded, since no larva was seen to use its TOs during the trials. Apparently the cap of glue precluded the eversion mechanism of the TOs, possibly because in the smaller caterpillars of *P. icarus* the edges of the DNO cap were too close to the TOs' sheath.

Thus, the strong reduction of the caterpillar-ant interactions might be due to the combined loss of both DNO and TOs. However, in feeding experiments with *P. icarus* on a nutrient-poor diet (*Robinia pseudoacacia*) a likewise drastic decline in myrmecophily was observed although the TOs remained fully functional there (Fiedler 1990c).

Polyommatus escheri — The few data obtained with only five individuals of this Mediterranean species permit just limited evaluation, even more so because the larvae were reared under a severe shortage of food. They did not accept any of several representatives of the family Fabaceae (*Onobrychis, Medicago, Hippocrepis, Trifolium*) as a substitute for their natural hostplant (*Astragalus monspessulanus* and allies) which was not sufficiently available. Given these premises, and in view of the finding that in *P. icarus* a sufficient larval nutrition is essential for the maintenance of ant-associations, the following data obviously represent nothing more than lower limits for the myrmecophily parameters of *P. escheri*.

Ants (*T. caespitum*) palpated the *P. escheri* caterpillars intensively, especially around the DNO. No attacks were observed. Three trials were made when the larvae were already in the prepupal stage and were thus no more able to evert their TOs or release secretions from the DNO.

The other five experiments yielded results somewhat intermediate between the two other *Polyommatus* species investigated (*coridon, icarus*; see Tab.2b). The mean frequency of palpation at the DNO within 30 min was rather low (13.60 ± 8.64, median = 18), and this may be attributed to the inability of the larvae to produce DNO secretions without appropriate food.

The eversion rate of the TOs, in contrast, was distinctly higher than in *P. icarus* (22.0 ± 14.35, median = 19). The myrmicine ant *T. caespitum*, however, showed no reaction on contacts with everted TOs. One larva successfully pupated during an experiment with constant attendance of 3—10 ants immediately before and after the moult.

Myrmecoxenous species

Lycaena phlaeas — Both ant species tested normally behaved peacefully towards caterpillars of *L. phlaeas*. However, most contacts lasted rather short and the ants usually only groped the larvae instead of typically palpating them (this distinction between groping [*Betasten*] and palpation [*Betrillern*] follows Malicky 1969b, 1970a). Real palpation was only occasionally observed and it normally waned soon, in particular with *L. flavus*. The ants' interest concentrated upon the PCO accumulations around the spiracles, especially on the prothorax and the 6th—8th abdominal segment. There the ants often nibbled with their mandibles, presumably harvesting the secretions.

Larvae of *L. phlaeas* only partially induced rather stable ant-associations (in 4 out of 16 trials with *L. flavus* and in 12 of 17 trials with *T. caespitum*). In 6 of 16 trials with *L. flavus* and in 1 of 17 with *T. caespitum*, individual ants tried to bite the caterpillar, but did not hurt it. Larvae thus attacked retracted their head under the prothoracic shield and repeatedly lifted their fore or rear end briefly, but showed no stronger defensive reaction (e.g. true thrashing).

Generally the myrmecophily parameters of *L. phlaeas* were significantly different from those of the *Polyommatus* species, with the single exception of larval attractiveness in experiments with *T. caespitum* (Tab.2).

Lycaena tityrus — Experiments with this species yielded very similar results. Indeed, the quantitative figures are in no case significantly different from those of *L. phlaeas* (Tab.2). As with the latter species, caterpillars of *L. tityrus* were mostly groped and only occasionally palpated.

Stable ant-associations were observed only twice in 14 experiments with *L. flavus*, but in 4 of 6 trials with *T. caespitum*. Faecal pellets produced by the caterpillars were highly attractive to *L. flavus*. Regularly 2—6 (maximum 12) ants chewed on such frass. On four occasions the frass received higher attendance than the larva itself, and ants were observed to leave the caterpillars to suck at their fresh faeces. The frass contained high amounts of amino acids (ninhydrine test).

Lycaena hippothoe — Caterpillars of this third *Lycaena* species were more intensively palpated than the two others, especially the large mature larvae. The latter

induced even stable ant-associations, but the larvae repeatedly showed defensive movements (brief lifting of fore or rear end) and retracted their head, or they even rolled up completely when visited by more than five ants.

Small younger last instars of *L. hippothoe*, in contrast, were treated in essentially the same way as caterpillars of *L. phlaeas* and *tityrus*. The combined data for all trials with *L. hippothoe* largely agree with those of the two other *Lycaena* species (Tab.2a).

The comparatively large faecal pellets (length 2—3 mm, ∅=1 mm) were extremely attractive to *Lasius flavus* ants. Six of eight frass pellets were chewed upon by 2—5 (maximum 15) ants, in one case for at least 22 min.

Callophrys rubi — Larvae of this member of the tribe Eumaeini were treated distinctly more aggressively by both ant species than *Polyommatus* or *Lycaena* caterpillars. *T. caespitum* never showed typical palpation, but brief groping at most, and *L. flavus* only very occasionally palpated *C. rubi* larvae for short periods. In 12 of 21 trials with *T. caespitum* and in 5 of 26 experiments with *L. flavus* some ants repeatedly tried to bite the *C. rubi* larvae. Twice a *T. caespitum* worker ant tightly clinged to a caterpillar for several minutes and even attempted to sting. In all these cases the caterpillars responded with defensive movements (brief lifting of the fore end, retraction of the head) and remained unhurt.

Although *C. rubi* larvae possess a DNO, no ants were ever observed to be attracted to this and actually I could never observe any DNO secretions. In summary, the larvae of *C. rubi* were very unattractive to both ant species and even rather often attacked. Their myrmecophily parameters were predominantly similar to those of the myrmecoxenous *Lycaena* species or even lower in part (Tab.2).

The frass pellets of *C. rubi* were highly attractive to *L. flavus* ants; 11 of 14 pellets were immediately visited by ants, whereas only three received no interest. On two occasions the ants took the frass directly from the larva's anus, and four faecal pellets were attended for 21—28 min.

Hamearis lucina — The larvae of *H. lucina* were totally unattractive to ants (tested only with *L. flavus*), but were regularly attacked. The ants tried to bite the larvae and exhibited a defensive posture after the first contacts.

Such attacks of *Lasius* ants against *H. lucina* larvae were already noted by Malicky (1969b). Several ants sat around one caterpillar with the mandibles opened and the gaster bent forward beneath the thorax. Even spraying of formic acid was confirmed on several occasions by its characteristic odour. Generally, the ants showed signs of alertness at the beginning of all experiments with *H. lucina*, but after the initial 5—10 min the larvae were largely ignored.

Caterpillars of this riodinid species differ from the lycaenids investigated in their dense coating with rather long and stiff hairs. Therefore the attacking ants were unable to hurt the caterpillars and when they grasped the ends of the long bristles, these were immediately released. In addition, the larvae showed defensive movements (short shaking of the head) and quickly crawled away when the ants became too harassing.

H. lucina caterpillars were the most active of all species tested, and their myrmecophily parameters were the lowest. In 7 of 11 cases the faecal pellets received considerable attendance of 1—8 ants for up to 10 min. The frass was in all these cases distinctly more attractive than the larva itself.

Tab.2: Quantitative results of experiments on interactions between caterpillars and ants. Given are means (standard deviations in parentheses). A: attractiveness of larvae; RV: coefficient of variation of A; P: permanence of ant-association; PT: arcsine-transformed values of P (definitions see text); n: number of experiments. -DNO: dorsal nectary organ of larvae rendered unfunctional. Figures of each column followed by different letters are statistically different (Mann-Whitney U-test, $p < 0.05$).

a) Experiments with *Lasius flavus*

	A	RV	P	PT	n
Polyommatus coridon	6.37 (1.59)a	0.061 (0.021)a	1.00 (0)a	90.00 (0)	24
P. coridon (-DNO)	2.77 (1.26)b	0.096 (0.038)b	0.93 (0.11)b	79.31 (12.02)	28
P. icarus	1.78 (0.82)c	0.152 (0.149)c	0.79 (0.17)c	66.31 (15.06)	26
P. icarus (-DNO)	0.65 (0.54)e	0.329 (0.146)e	0.41 (0.24)e	39.43 (14.94)	20
Lycaena phlaeas	1.36 (1.00)d	0.210 (0.062)d	0.59 (0.18)d	50.61 (11.45)	16
L. tityrus	0.91 (0.75)de	0.278 (0.145)de	0.51 (0.26)de	46.82 (18.88)	14
L. hippothoe	1.97 (2.10)cd	0.236 (0.177)cd	0.63 (0.33)d	57.11 (25.46)	17
Callophrys rubi	0.81 (0.59)e	0.290 (0.165)de	0.45 (0.23)e	41.80 (14.77)	26
Hamearis lucina	0.62 (0.33)e	0.263 (0.085)e	0.43 (0.17)e	41.00 (10.46)	24

b) Experiments with *Tetramorium caespitum*

	A	RV	P	PT	n
Polyommatus coridon	10.16 (2.23)a	0.063 (0.009)a	0.99 (0.02)a	88.72 (4.43)	12
P. icarus	3.89 (2.55)b	0.079 (0.054)a	0.94 (0.15)a	83.22 (13.98)	38
P. escheri	3.35 (2.32)b	0.095 (0.056)b	0.92 (0.16)ab	80.37 (15.61)	8
Lycaena phlaeas	3.14 (2.69)b	0.118 (0.061)b	0.84 (0.19)b	71.64 (17.24)	19
L. tityrus	2.46 (1.54)b	0.144 (0.105)b	0.79 (0.32)b	72.67 (26.91)	6
Callophrys rubi	2.57 (1.50)b	0.118 (0.068)b	0.84 (0.22)b	74.39 (19.59)	21

Discussion

The function of the myrmecophilous organs

Pore cupola organs (PCOs) — The above experiments yielded additional information about the role of the three major types of myrmecophilous organs found on lycaenid larvae. With regard to the PCOs, it is apparent that these organs are attractive to ants in the genera *Polyommatus* and *Lycaena*, but not in *Callophrys rubi* and *Hamearis lucina*. The latter two species were rarely if ever palpated at their PCOs.

These findings quantitatively confirm the qualitative statement of Malicky (1969b) that considerable differences exist in the attractiveness of lycaenid immatures to ants. The

most likely explanation of such differences is that the PCO-secretions of the species investigated differ in their chemical composition. The low attractiveness of *C. rubi* and *H. lucina* larvae even raises the question as to whether the PCOs of these species release any ant-related secretions at all, and generalizations regarding the function of the PCOs and their secretions should thus be seen with caution. DeVries (1988) and Harvey (1989) could not detect any attractiveness of the PCOs of several riodinids.

Thus, although it is currently generally accepted that the PCOs play an important role in the avoidance of ant-attacks (Malicky 1969b) or even serve as attractive glands with possibly nutritive secretions (Pierce 1983, 1989), this view urgently needs substantiation by chemical investigations on a broader spectrum of species. Obviously, the ant-attracting or appeasing function of the PCOs is not a universal trait common to both the Riodinidae and Lycaenidae, but is restricted to one subfamily, viz. the Lycaeninae.

The PCOs even differ in their attractiveness to ants among related species, or among individuals of the same species. *P. coridon* larvae were always palpated much more intensively than those of *P. icarus*, and in the DNO-exclusion experiments *P. coridon* larvae still induced ant-associations, whereas *P. icarus* did not. In the recruitment experiments of Fiedler & Maschwitz (1989a) with *P. coridon*, caterpillars with a capped DNO likewise partially retained their attractiveness and released a weak residual recruitment response.

Solicitation of weak food recruitment was also observed with *P. coridon* pupae that only possess PCOs (Fiedler 1988a, Fiedler & Maschwitz 1989a). Pupae of *P. icarus* and *P. escheri*, too, were steadily palpated and decidedly attractive to ants (Fiedler, unpublished), and several *Polyommatus* species (e.g. *coridon, bellargus, icarus*) are known to be associated with ants (mainly of the genus *Lasius*) during the pupal stage in the field (Thomas 1983, Emmet & Heath 1990). All these observations suggest that species- and instar-specific, or even individual differences of the PCO-secretions do occur amongst the genus *Polyommatus*.

Within the genus *Lycaena* the results are likewise indicative of a variable attractiveness of the PCOs. In all three *Lycaena* species investigated, some larvae induced rather stable ant-associations while others did not. Large caterpillars of *L. hippothoe* were nearly always attractive, but in *L. tityrus* and *L. phlaeas* the attractiveness was usually rather low.

Corresponding results have been obtained with other species of *Lycaena*. Malicky (1969b) noted, without reporting quantitative details, that caterpillars of *L. virgaureae* and *L. dispar* were often attractive to ants. In his experiments *L. phlaeas, L. tityrus* and *L. hippothoe* were only weakly attended by ants. Elfferich (1963b, and pers. comm.) found caterpillars of *Lycaena dispar* and *L. ottomanus* attractive to the ant *Lasius niger*, whereas a *Myrmica* species showed no interest. Again *Lycaena phlaeas* and *L. tityrus* were usually unattractive. In addition to the results reported above I have observed strong palpation behaviour and permanent associations in laboratory trials with fully grown caterpillars of *Lycaena alciphron* and the ant *Lasius brunneus*.

The pattern thus emerging is that a number of *Lycaena* species have the potential to attract ants to some degree with the help of their PCOs, but that this attractiveness is

not realized in all individuals. As a consequence, ant-associations of *Lycaena* larvae have only occasionally been observed in the field (from Europe there are only single records for *L. dispar*: Hinton 1951, Ebert & Rennwald 1991). In four myrmecophilous *Lycaena* species from North America additional attractive organs (viz. dendritic setae) are involved (Ballmer & Pratt 1988, and in press).

Anyway, the PCOs apparently permit a fine tuning of the attractiveness of lycaenid caterpillars towards ants without major changes in morphology. The mechanisms underlying this intrageneric or even intraspecific variability require further study.

Dorsal nectary organ (DNO) — The exclusion experiments confirmed the paramount importance of the DNO for the maintenance of stable ant-associations. *Polyommatus coridon* and *P. icarus* caterpillars with their DNO rendered unfunctional received distinctly less attention by ants, and the latter became even functionally myrmecoxenous. This finding contradicts the work of Malicky (1969b) who performed similar exclusion experiments, but could not observe differences in the ant behaviour following DNO-exclusion. This is clearly one aspect where the use of quantitative comparative studies provided a significant progress: without a statistical treatment the differences are sometimes difficult to detect.

As with the PCOs, the experiments revealed a considerable disparity in the function of the DNO between *P. coridon* and *P. icarus*. *P. coridon* caterpillars produce DNO secretions steadily throughout their 3rd and 4th instar at an average rate of about 30 droplets/h when mature. The palpation intensity at the DNO was rather similar with all larvae tested, suggesting that the secretory activity of *P. coridon* caterpillars of similar age varies little. *P. icarus*, in contrast, produced significantly fewer DNO secretions with an estimated rate of about 6 droplets/h. In addition, such secretions were regularly seen only during the last 2—3 days prior to pupation. Younger larvae (e.g. 3rd instars) very rarely released DNO secretions and accordingly they were even less intensively visited (Fiedler, unpublished).

Furthermore, the higher variance of the palpation frequency at the DNO indicates that the activity of this organ is much more variable in *P. icarus* larvae than in *P. coridon*. Differences in the nutritive quality of the actual larval hostplant could be partly responsible for this variability (Fiedler 1990c, Baylis & Pierce 1991).

In *P. icarus* the DNO-palpation frequency was significantly correlated with the myrmecophily parameters A, RV, and P (experiments with *L. flavus*; A: $r_S = 0.60$; RV: $r_S = -0.64$; P: $r_S = 0.664$; $p < 0.001$). In other words, larvae with an attractive DNO had the highest overall attractiveness and thus maintained stable and permanent ant-associations. In *P. coridon* no such correlations were found.

This is a further piece of evidence that a functional DNO is essential for the myrmecophily of *P. icarus*. Remarkably the caterpillars of *Callophrys rubi*, although possessing a DNO, were totally unattractive for both ant species. Indeed, no single secretion act could be observed with these larvae, and morphological examinations with the SEM revealed that most likely the DNO of *C. rubi* is rudimentary (Fiedler 1990d).

Malicky (1969b) has already noted that in some Eumaeiti larvae the DNO appears to be non-functional (e.g. *Strymon melinus, Satyrium acaciae*), and Ballmer & Pratt (in press) could not observe DNO secretion acts in 18 Californian species of the same subtribe.

This indicates that in some Eumaeiti the myrmecophilous organs show a marked tendency towards reduction, a character that will be discussed in detail later on. An important corollary of this findings is that it does not suffice to simply determine the presence or absence of the DNO in order to distinguish between myrmecophilous and myrmecoxenous species. This approach of Kitching & Luke (1985) has to be modified in that only lycaenid caterpillars with a **functional** DNO are likely to be attended by ants in the field.

Tentacle organs (TOs) — The experiments with *Polyommatus coridon* and *P. icarus* confirmed that the TOs of these species are able to alert certain formicine ants like *Lasius flavus* whereas the myrmicine ant *Tetramorium caespitum* showed no reaction. For both *Polyommatus* species this had been observed earlier (Elfferich 1963b, Fiedler & Maschwitz 1988b).

The TOs of *P. coridon* were more effective, and caterpillars of this species also evert their TOs more frequently than *P. icarus*. Apparently the signal produced by *P. icarus* is weaker than that of *P. coridon*. According to Elfferich (1963b) caterpillars of *P. icarus* elicit excited runs more effectively in the ant *Lasius niger* than in *L. flavus*.

As suspected earlier (Fiedler & Maschwitz 1988b), the eversion rate of the TOs was indeed significantly correlated with the permanence of associations between *P. icarus* larvae and *L. flavus*, supporting the view that the TOs may enhance and modify ant-associations of lycaenid caterpillars in general.

Another interesting observation was that the TOs rapidly loose their ability to alert ants when extruded for a longer time (more than 20 s). Usually everted TOs are detected or touched by attendant ants within seconds and are then immediately retracted. In DNO-exclusion experiments with *P. icarus*, however, the larvae had so little ant-attendance that sometimes a TO remained everted for up to one minute. When an ant encountered such a long-everted TO, it did not react at all and the TO was eventually retracted.

This observation indicates that the TOs may release a volatile signal that quickly evaporates. Similar results were obtained by Ballmer & Pratt (in press) with the North American *Plebulina emigdionis*. Caterpillars of this species often crawl about with everted TOs for several minutes, and ants (*Formica pilicornis*) are not alerted then. The same ant species readily reacted upon contact with the TOs of a number of related Californian *Plebejus* species.

It remains unknown whether the dendritic hairs on the top of the TOs produce and release the presumed volatile signal or simply serve as dissipative structures. In the latter case the allomone might be produced in the sheath of the TOs, and this could explain why Malicky (1969b) did not find glandular elements on the TOs.

Anyway, these observations are in accordance with the hypothesis that ant alarm-pheromones or mimics of those might be released by the TOs. Alarm-pheromones of ants are usually blends of multiple components (e.g. Bradshaw et al. 1979), and often one such component is used in a rather wide taxonomic range of ants (Hölldobler & Wilson 1990). This would explain why formicine ants of the genera *Lasius* or *Plagiolepis* respond to the TOs of *Polyommatus* caterpillars, whereas myrmicine ants like *Myrmica* and *Tetramorium* do not.

However, the reaction of *Tapinoma* ants (Dolichoderinae) to the TOs of *Polyommatus (Lysandra) golgus, P. nivescens*, and *Aricia morronensis* (Munguira & Martín 1988, 1989b) does not fit well into this hypothesis since the alarm substances of *Tapinoma* are chemically quite different (Hölldobler & Wilson 1990). Detailed investigations on the chemical nature of the signals produced by the TOs are clearly needed to further test the alarm-pheromone hypothesis, even more so since Malicky (1969b) has strictly rejected any glandular function of the TOs.

Comparative aspects

The quantitative investigations of the interactions between several European lycaenids and two ant species yielded one consistent result: the myrmecophily parameters differed significantly between myrmecophilous and myrmecoxenous caterpillars. This distinction was hitherto based mainly on the occurrence of the DNO and the presence of records of ant-associations in the field (Kitching & Luke 1985).

The existence of stable ant-associations in the field is unambiguously the ultimate and ecologically relevant criterion in this distinction. However, such final designations require thorough and time-consuming field work that has been done for far less than 50 lycaenid species from genera like *Lycaena, Jalmenus, Ogyris, Callophrys, Glaucopsyche, Maculinea, Plebejus, Polyommatus* (e.g. Wright 1983, Thomas 1983, 1985a, b, Thomas et al. 1989, Pierce & Elgar 1985, Pierce et al. 1987 etc.). Furthermore, field records are available only for a limited number of species and many records, for tropical species in particular, are based on single rearings or field observations, such data usually not permitting any direct comparisons.

Even in the better known European fauna, sufficient life-history information is available for only a fraction of the lycaenids. In addition, it is sometimes difficult to conclude from the literature records whether observed ant-associations are a regular phenomenon or only occur occasionally. Accordingly, species like *Lycaena dispar* or *Callophrys rubi* were repeatedly categorized as myrmecophilous on the grounds of single old records (e.g. Warnecke 1932/33, Hinton 1951, Kitching & Luke 1985), while more recent studies either did not mention myrmecophily as a significant factor (*L. dispar*: Duffy 1968), or even demonstrated that ant-associations are exceptional events at most (*C. rubi*: Fiedler 1990d).

Given the large species diversity of the Lycaenidae and the considerable difficulties associated with field studies on their larval ecology, thorough ecological investigations of a taxonomically representative number of species are beyond reach. Thus, future research must further largely pertain to the description of life-histories, while the

necessary detailed ecological and physiological studies will unevitably remain restricted to a small number of "model species".

Hence, comparative investigations using the myrmecophily parameters described above may turn out extremely useful, because they rather rapidly yield data on the extent of ant-associations in a number of species. For the progress in understanding the evolution of lycaenid-ant interactions, such a more complete comparative knowledge is crucial.

Using the myrmecophily parameters A, RV, and P the caterpillar species investigated are divided into four groups. *P. coridon* was highly myrmecophilous, *P. icarus* more weakly ant-associated (with all myrmecophilous organs less attractive and less active than in *P. coridon*), the *Lycaena* species were myrmecoxenous and only partially induced ant-associations, and *Callophrys rubi* as well as the riodinid *Hamearis lucina* were totally unattractive to ants and were sometimes even attacked. *P. escheri* (see above) and *P. daphnis* (Fiedler, unpublished) likewise belong to the distinctly ant-attractive species.

Malicky (1969b), in his extensive studies using a larger number of European lycaenid species, gave few quantitative details of his experiments. Nevertheless, it is possible to compare some of his results with this categorization. According to his Tab.5 (Malicky 1969b:261) the following species are highly attractive to ants:

The polyommatines *Celastrina argiolus, Scolitantides orion, Pseudophilotes schiffermuelleri, Plebejus argus, P. (Lycaeides) idas, P. (L.) argyrognomon, Polyommatus (Aricia) agestis, P. (Agrodiaetus) damon, P. (Lysandra) dorylas, P. (Meleageria) daphnis*, and perhaps *Satyrium spini* (Eumaeiti). All these species possess a functional DNO and (with the exception of *S. spini*) a pair of TOs. *P. damon* and *P. dorylas* apparently everted their TOs less frequently than the remaining species, but for *P. dorylas*, at least, the alerting function of the TOs has been observed in the field (Munguira & Martín 1989b). Furthermore, all these species have well-known ant-associations in the field (see Appendix), although in *C. argiolus* ant-associations are seemingly not universal (Harvey & Webb 1980, Emmet & Heath 1990).

Judging from Malicky's data the following species belong to the second group with rather weak myrmecophily:

The Eumaeiti species *Satyrium w-album, S. ilicis*, and possibly *S. acaciae*, as well as *Polyommatus amandus* and *P. thersites*. All of them have well established ant-associations in the field and possess a functional DNO (see Appendix) with the exception of *S. acaciae*. The latter has apparently never been found with ants, and at another place Malicky (1969b:248) notes that the DNO of its larvae may be rudimentary.

The third group comprises the Theclini species *Thecla betulae* and *Quercusia quercus*, the *Lycaena* species *phlaeas, tityrus, virgaureae, dispar* and *hippothoe*, and the Eumaeiti species *Satyrium (Fixsenia) pruni*. Caterpillars of these species were sometimes found to be attractive and were in part intensively palpated, but all lack a functional DNO (Malicky states that *S. pruni* has a DNO, but SEM studies of Kitching & Luke [1985] proved this organ to be absent). Correspondingly, larvae of all these species have never or only very occasionally been found associated with ants in the field.

The totally unattractive species were the same as in my experiments, viz. *Callophrys rubi* (Malicky 1969b:278) and *Hamearis lucina* (loc. cit.:266).

Thus, despite the lack of quantitative data and the use of different ant species, the experimental results of Malicky (1969b) largely agree with the categorization obtained from my laboratory studies. In addition, these categorization corresponds astonishingly well to the field data available, giving further support to the applicability of the experimental method developed here.

A direct comparison with the results of Ballmer & Pratt (in press) is more difficult, mainly due to the different experimental procedure. Ballmer & Pratt confronted one caterpillar with five ants (*Formica pilicornis*) for 5 min and only recorded the permanence of ant-associations (defined as the percentage time a caterpillar had contact with ants).

Nevertheless, the Californian species investigated can be grouped into three categories. Highly myrmecophilous caterpillars are visited by ants more than 90 % of the experimental time (e.g. three *Lycaena* species, *Harkenclenus titus, Phaeostrymon alcestis*, 6 *Satyrium* species, and 13 of 22 Polyommatini), and most of these have been recorded with ants in the field.

Moderately to weakly attractive were some *Callophrys* species, *Satyrium fuliginosum, Fixsenia ontario*, and four Polyommatini species. Distinctly unattractive were eight myrmecoxenous *Lycaena* species, the Thecliti genera *Habrodais* and *Hypaurotis*, four Eumaeiti species, and two myrmecoxenous riodinids. In all, this grouping rather well parallels the occurrence of ant-association in the field, but the congruence is less perfect than in the species covered in the present study.

Most likely, this is due to limitations of the experimental design employed: the focus on the short-time aspects of caterpillar-ant interactions may well mask distinct differences in the attractiveness of the caterpillars. Of course, the interpretation of laboratory results must always be done with caution, but the evaluation of the results of Malicky, of Ballmer & Pratt, and of this study shows that meaningful conclusions can be drawn with regard to the presence and extent of ant-associations in the field.

LYCAENID SYSTEMATICS AND MYRMECOPHILY

The system of the Lycaenidae

Previous studies of myrmecophily in the Lycaenidae were either based on now outdated higher classifications of the family (Warnecke 1932/33, Malicky 1969b), or they decidedly rejected any possible relations between higher classification and evolution of ant-associations (e.g. Pierce & Elgar 1985, Pierce 1987). It is one central aim of this study to show that, using a modern approach to the higher classification of the family Lycaenidae, important correlations between myrmecophily and systematics become obvious.

In the following I will first give a brief account of the classification upon which this study is based. The second part of this chapter deals with the occurrence of ant-associations and myrmecophilous organs in the various subgroups of the Lycaenidae, and the third part gives a short characterization of all major lycaenid taxa with respect to myrmecophily.

The higher classification of the Lycaenidae is still far from being resolved in a thoroughly phylogenetic sense. Like in the second large butterfly family Nymphalidae (cf. Ackery 1988), a number of well defined and very probably monophyletic taxa exist in the Lycaenidae, but their exact relationships to each other are not yet sufficiently clear. The classical study of Eliot (1973) provides the basis for all modern approaches to Lycaenidae systematics. Scott & Wright (1990) rearranged and somewhat harmonized this classification, and I largely adopt this with only minor alterations (Tab.3).

According to this system the Lycaenidae consist of the 4 subfamilies Poritiinae, Miletinae, Curetinae, and Lycaeninae. The Riodinidae, often treated as a subfamily of the Lycaenidae (e.g. Scott 1985, Scott & Wright 1990), are here viewed as a distinct family. Harvey (1987) proposed the Riodinidae being the sister-group of the Lycaenidae, but according to Robbins (1988a) the Riodinidae may rather form a monophyletic unit together with the Nymphalidae.

Furthermore, the riodinids have followed an entirely convergent, but not homologous evolutionary pathway with respect to myrmecophily (DeVries 1990b). Therefore, the treatment of the riodinids as a distinct family avoids the possible paraphyly of the Lycaenidae s.l. (i.e. including the riodinids).

The remaining lycaenid subfamilies are still not of identical rank in a cladistic system, but a more sophisticated hierarchy must await further analysis. For a detailed account of all relevant morphological characters the reader is referred to Eliot (1973), Scott (1985), Harvey (1987), Robbins (1988a, b), and Scott & Wright (1990). Stempffer's (1967) and Eliot's (1973) treatises also encompass historical perspectives of lycaenid systematics. The present study is not intended to revise the classification of the Lycaenidae, and in the following I only briefly discuss those characters related to myrmecophily.

The Poritiinae and Miletinae lack a number of apomorphic characters of the Lycaeninae and are thus usually viewed as the earliest branches of the Lycaenidae. Several

Tab.3: The higher taxa of the Lycaenidae (modified from Scott & Wright 1990) with approximate species numbers (after Bridges 1988), numbers of species with life-history information available (percentage in brackets), and main area of distribution.
*: Larvae with only dorsal nectary organ (DNO) recorded;
+: larvae with DNO and tentacle organs (TOs);
T: only TOs present.

a) Lycaenid subfamilies, and Poritiinae and Miletinae tribes

Taxon	Species number	Life-history information	Main distribution
Poritiinae	572	59 (10.3)	Palaeotropical
Poritiini	52	1 (1.9)	Oriental
Liptenini	520	58 (11.2)	African
Miletinae	140	37 (26.4)	Palaeotropical
Miletini	120	28 (23.3)	Oriental
Liphyrini T	20	9 (45.0)	African
Curetinae T	18	6 (33.3)	Oriental
Lycaeninae +	3640	968 (26.6)	Cosmopolitan
Aphnaeini +	253	77 (30.4)	African
Lycaenini	92	38 (41.3)	Holarctic
Theclini +	530	120 (22.6)	Palaeotropical
Eumaeini +	1580	367 (23.2)	South Hemisphere
Polyommatini +	1182	366 (31.0)	Old World

b) Theclini subtribes

Taxon	Species number	Life-history information	Main distribution
Luciiti +	149	43 (28.9)	Australian
Ogyriti +	15	12 (80.0)	Australian
Zesiiti +	11	11 (100)	Australian
Arhopaliti +	236	20 (8.5)	Oriental
Thecliti (*)	119	34 (28.6)	Sino-Oriental

c) Eumaeini subtribes

Taxon	Species number	Life-history information	Main distribution
Catapaecilmatiti +	11	2 (18.2)	Oriental
Amblypodiiti +	13	8 (61.5)	Palaeotropical
Oxyliditi ?	8	0	African
Hypothecliti ?	3	0	Australian
Loxuriti +	57	11 (19.3)	Oriental
Iolaiti +	206	64 (31.1)	Palaeotropical
Remelaniti *	7	2 (28.6)	Oriental
Hypolycaeniti *	53	13 (24.5)	Palaeotropical
Deudorigiti +	200	46 (23.0)	Palaeotropical
Eumaeiti *	1023	221 (21.6)	Neotropical

d) Subtribes and sections of the Polyommatini

Taxon	Species number	Life-history information	Main distribution
Candaliditi +	30	14 (46.7)	Australian
Lycaenesthiti +	136	33 (24.3)	African
Niphanditi +	6	1 (16.7)	Oriental
Polyommatiti +	1010	318 (31.5)	Old World
Cupidopsis	3	2 (66.7)	African
Nacaduba	146	29 (19.9)	Oriental
Jamides	91	12 (13.2)	Oriental
Uranothauma	42	19 (45.2)	African
Leptotes	23	9 (39.1)	African
Castalius	37	21 (56.8)	Palaeotropical
Zizeeria	19	14 (73.7)	Palaeotropical
Everes	77	27 (35.1)	Old World
Lycaenopsis	113	15 (13.3)	Oriental
Glaucopsyche	53	33 (62.3)	Holarctic
Euchrysops	175	49 (28.0)	African
Polyommatus	231	88 (38.1)	Palaearctic

characters indicate that Poritiinae and Miletinae may be sister-groups (Scott & Wright 1990, Eliot, pers. comm.).

The Poritiinae consist of two tribes, the Oriental Poritiini (> 50 spp.; all species numbers are approximate figures based on the catalogue of Bridges 1988) and the African Liptenini (>520 spp.). The Liptenini are further subdivided into three subtribes (Pentiliti, Durbaniiti and Lipteniti).

The largely Palaeotropical Miletinae, as well, comprise two tribes, the Miletini (120 spp., including the subtribes Spalgiti, Tarakiti, Miletiti and Lachnocnemiti) and the mainly African Liphyrini (20 spp.). Eliot (pers. comm.), however, relates the Lachnocnemiti with the Liphyrini.

The systematic position of the third Oriental subfamily Curetinae (18 spp.) is still uncertain. Previously sometimes even treated as a distinct family (Shirôzu & Yamamoto 1957), the Curetinae have later been placed at various positions within the Lycaenidae. Scott (1985) suggested the Curetinae to be the sister-group of the Riodinidae, whereas Scott & Wright (1990) claim a sister-group relationship with the Lycaeninae. Robbins (1988a), however, provided evidence that the Curetinae might form a monophyletic unit together with the Poritiinae and Miletinae, and Eliot (pers. comm.) supports this latter view. Anyway, the Curetinae (consisting only of the genus *Curetis*) possess a number of highly apomorphic characters together with some primitive features which makes a final decision yet impossible.

The last and by far most species-rich subfamily are the Lycaeninae (3640 spp.). They have a worldwide distribution and are further subdivided into 5 tribes. Only three of these are well defined monophyletic taxa: Aphnaeini, Lycaenini, and Polyommatini.

The Lycaenini comprise less than 100 predominantly Holarctic species, and the largely African Aphnaeini contain about 250 species.

The monophyly of the third tribe Theclini (c. 530 spp.) is questionable. Previous classifications (e.g. Eliot 1973) used the name "Theclinae" in an even much broader sense, but this assemblage appears to be paraphyletic (Scott & Wright 1990). The Theclini, as defined by Scott & Wright (1990), are grouped into five subtribes with characteristic distributional patterns (Tab.3): Luciiti, Ogyriti, Zesiiti, Arhopaliti, and Thecliti.

The phylogenetic relationships among these subtribes are unclear. Luciiti, Ogyriti and Zesiiti are rather isolated and presumably old, mainly Australian lineages, wheras Arhopaliti and Thecliti together possibly constitute a monophyletic unit (Eliot, pers. comm.), the Thecliti being the temperate Asian equivalent to the tropical Oriental Arhopaliti.

The fourth and most diverse tribe are the Eumaeini (c. 1580 species). The systematics of this group as well as its monophyly are poorly documented. The Eumaeini roughly fall into two groups: a number of subtribes in the Old World, and the largely Neotropical Eumaeiti (> 1000 species).

The latter are monophyletic and are represented in the northern hemisphere with only about 60 species each in the Nearctic and Palaearctic region, respectively. More than 900 Eumaeiti species are strictly Neotropical, and their systematics and ecology are in urgent need of further work (Robbins, pers. comm.). The Old World Eumaeini subtribes are split into a number of taxa according to Eliot (1973) and Scott & Wright (1990). However, Eliot himself (in Corbet & Pendlebury 1978) has questioned the validity of several of these separations.

For the purpose of this study I here lump together some of these, using suggestions of Eliot (pers. comm.). Accordingly, the Old World Eumaeini consist of the subtribes Catapaecilmatiti, Amblypodiiti, Oxyliditi, Hypothecliti (perhaps better placed in the Theclini?, Eliot, pers. comm.), Loxuriti (including the Cheritriti and Horagiti sensu Scott & Wright 1990; see Corbet & Pendlebury 1978), Iolaiti, Remelaniti, Hypolycaeniti, and Deudorigiti (including Tomariti). There is some evidence that Deudorigiti and Eumaeiti are sister-groups, but the phylogenetic relationships of the remaining subtribes to each other are unknown.

I have largely adopted this subdivision simply in the absence of better alternatives, and further research may well reveal that the Eumaeini subdivision adopted here goes too far. Also, some of the taxa included may turn out to be more closely related to what is here termed "Theclini".

The last tribe of the subfamily Lycaeninae are the Polyommatini (> 1180 species). They are very probably monophyletic and can further be subdivided into four subtribes (Candaliditi, Lycaenesthiti, Niphanditi, and Polyommatiti). The Polyommatiti are by far the largest of these (> 1000 species) and were grouped in a number of sections by Eliot (1973). Again Eliot's subdivision created a number of very small taxa of somewhat

questionable significance, and I have tentatively grouped those together where a clear relationship was indicated by Eliot (1973).

The following sections are recognized within the Polyommatiti: *Cupidopsis* section, *Nacaduba* section (including the *Petrelaea, Theclinesthes, Upolampes* and *Danis* sections of Eliot), *Jamides* section (including *Catochrysops* and *Lampides* sections), *Uranothauma* section (including *Phlyaria* and *Cacyreus* sections), *Leptotes* section, *Castalius* section, *Zizeeria* section (including *Zintha, Famegana, Actizera, Zizula* and *Brephidium* sections), *Cupido* section (including *Pithecops, Azanus* and *Eicochrysops* sections), *Lycaenopsis* section, *Glaucopsyche* section, *Euchrysops* section, and *Polyommatus* section (see Tab.3).

Tab.3 summarizes this systematic approach. It must be emphasized again that the higher classification of the Lycaenidae as suggested here is not yet a truly phylogenetic one. However, this classification likely parallels the phylogeny of the Lycaenidae more closely than all pre-Eliotian attempts.

As will be seen later, this classification, albeit mainly based on adult morphological characters, is in surprisingly good agreement with the zoogeography of the lycaenid subgroups and the information available on morphology and biology of the early stages. It seems thus feasible to base the discussions of lycaenid myrmecophily on this approach, but one should always keep in mind that future research on the cladistics of the Lycaenidae will certainly lead to a number of improvements and changes.

Systematic distribution of myrmecophilous organs within the Lycaenidae

Most approaches to the higher classification of the Lycaenidae, including Scott & Wright (1990), assume that myrmecophily is an ancestral character of the family. As a logical consequence, all cases where neither myrmecophilous organs nor ant-associations are present must be viewed as secondary losses in such scenarios. In other words: myrmecoxeny within the Lycaenidae would always be a secondary trait.

This paragraph is devoted to the question which lycaenid taxa possess what types of myrmecophilous organs and ant-associations. As a result the hypothesis of ancestral myrmecophily and the systematic position of some lycaenid taxa will be critically re-examined.

The outgroups: Nymphalidae and Riodinidae

Any interpretation of a character state as plesiomorphic or apomorphic in a phylogenetic context must imply the outgroup comparison as most important methodology (Hennig 1982, Ax 1984). Irrespective of the detailed position of the Riodinidae, most modern authors (e.g. Kristensen 1976, Scott & Wright 1990) agree that Lycaenidae, Riodinidae and Nymphalidae together constitute a monophyletic taxon. Likewise, there is broad agreement that the Nymphalidae are monophyletic.

Thus there are two outgroups that should be considered with respect to the ancestral Lycaenidae, viz. the Nymphalidae and the Riodinidae. In the large family Nymphalidae

no single case of larval myrmecophily is known, nor does any known nymphalid larva possess any myrmecophilous organs. Unless one assumes that the ancestor of all Nymphalidae has lost its myrmecophily, the unavoidable and most parsimonious interpretation is that the ancestor of the nymphalids as well as that of the whole group Nymphalidae + Riodinidae + Lycaenidae was primarily myrmecoxenous, as are all other Papilionoidea.

Within the Riodinidae myrmecophilous organs and ant-associations are known or suspected from quite a number of species. However, the larval myrmecophilous organs of the Riodinidae are structurally and functionally different from those of the Lycaenidae and occur in different locations (Ross 1964, Cottrell 1984, DeVries 1988, 1990). They are hence viewed by DeVries (1990b) as analogous, but not homologous structures of the caterpillars. In addition, myrmecophily within the Riodinidae is confined to the tribes Eurybiini, Lemoniini and Nymphidiini of the subfamily Riodininae. These tribes are considered as the most advanced of the whole family, representing less than an estimated 300 species (Harvey 1987).

Accordingly, myrmecophily and the possession of ant-organs are viewed as an apomorphic character state of these three tribes, whereas taxonomic groups such as Hamearinae, Euselasiinae, and five Riodininae tribes entirely lack ant-associations and myrmecophilous organs. The latter taxa share a number of other independent plesiomorphic traits and are thus believed to have split off from the stem group of the higher Riodininae prior to the evolution of myrmecophily (Harvey 1987). This taxonomic distribution of ant-associations provides strong evidence that the ancestral Riodinidae were primarily myrmecoxenous.

With respect to the presumed sister-group relationship between Riodinidae and Lycaenidae this conclusion implies that a number of characters related to myrmecophily are not synapomorphies of the Lycaenidae + Riodinidae as a whole. Examples taken from Scott & Wright (1990) are: the thick larval cuticle (which is not typical for riodinid caterpillars); the ability to retract the head beneath the prothorax (typical for Lycaeninae larvae, but only weakly developed in the Riodinidae and in several lycaenid lineages); the tentacle organs on the eighth abdominal segment (missing in all primarily myrmecoxenous riodinids, structurally and functionally different in myrmecophilous riodinids); the dorsal nectary organ (totally absent in all riodinids); and the preference of the larvae for young plant tissue, flowers or fruits (riodinids generally feed on mature leaves, only myrmecophilous species tend to prefer plants bearing extrafloral nectaries and even utilze this nectar: Harvey 1987, DeVries 1990b, DeVries & Baker 1990).

The only type of larval organs related to myrmecophily that is common to both Riodinidae and Lycaenidae are the pore cupola organs (PCOs) or "lenticles". However, as already explained in the introduction, the PCOs of riodinids, including myrmecophilous species, are not attractive to ants (DeVries 1988, Harvey 1989). Therefore, even if the PCOs are a synapomorphy of Riodinidae and Lycaenidae (Harvey 1987), their connection to myrmecophily is almost certainly restricted to the Lycaenidae s. str. (experimental evidence for the ant-attractiveness of the PCOs is even restricted to the subfamily Lycaeninae). The ancestral function of the PCOs remains unknown.

Summarizing the above arguments, the outgroup comparisons with the Nymphalidae and Riodinidae lend no support to the idea that these two taxa were primarily myrmecophilous, irrespective of their detailed phylogenetic relationships to the Lycaenidae.

The subfamilies Poritiinae, Miletinae, and Curetinae

It is generally accepted that Poritiinae and Miletinae are the earliest offshoots form the common ancestral Lycaenidae stem. The presence of PCOs in the Poritiinae is very likely (see Clark & Dickson 1971), but requires confirmation. There is no indication that any Poritiinae larva hitherto known possesses either a DNO or a pair of TOs. Instead, Poritiinae caterpillars are usually hairy (at least in later instars), and in the Riodinidae hairiness is markedly correlated with myrmecoxeny (DeVries 1990b).

Larvae and pupae of the Miletinae (except the highly specialized *Liphyra brassolis*) possess PCOs, although their morphology differs from the types found in the Lycaeninae and some Riodinidae (Kitching 1987; Fiedler, unpublished). A DNO has not been observed in the Miletinae, but Kitching (1987) mentions a structure on the seventh abdominal segment of *Allotinus major* that he calls "pseudo-Newcomer's organ". However, the glandular nature of this structure has not been proved, and many Miletinae caterpillars are not attractive for ants, but are either sometimes attacked (*Feniseca, Spalgis?*) or largely ignored by ants (see below).

TOs on the eighth abdominal segment are only known from one African Liphyrini genus, *Aslauga* (Jackson 1937, Boulard 1968, Cottrell 1981, 1984, Villet 1986). Lamborn (1914) observed that these TOs "are thrust out from time to time", but he did not mention any relation to the presence of ants.

In summary, the larvae of both, the Poritiinae and Miletinae, lack the typical myrmecophilous organs of higher lycaenids except the seemingly ubiquitous PCOs. The isolated occurrence of TOs of unknown function in one single genus (*Aslauga*) is indicative of an independent evolution of this character rather than of an ancestral equipment with TOs that were subsequently lost in all Poritiinae and the vast majority of the Miletinae (Eliot, pers. comm.).

The placement of the Curetinae is still discussed controversially (see above). Anyway, whether they are interpreted as the sister-group of the Lycaeninae (Scott & Wright 1990), as a part of a taxon comprising Poritiinae, Miletinae and Curetinae (Robbins 1988a), or even as the earliest offshoot of the Lycaenidae as a whole (Eliot, pers. comm.), all these interpretations view this subfamily as ancestral in relation to the Lyaeninae.

Larvae and pupae of its only genus *Curetis* possess strikingly aberrant epidermal organs. The functions of these organs (e.g. "perforated chambers": DeVries et al. 1986) remain unknown. PCOs are present, but their structure is unique in the larvae (DeVries et al. 1986), and the pupal PCOs can only be recognized as such on the grounds of their locations (Fiedler, unpublished). A DNO is not known from *Curetis* larvae. Instead they possess a specialized groove of unknown function between the abdominal segments 7 and 8 (DeVries et al. 1986). As with the "pseudo-Newcomer's organ" of *Allotinus* it is

unclear and rather unlikely whether this organ of *Curetis* is homologous to the true DNO of the Lycaeninae (Scott & Wright 1990, Eliot, pers. comm.).

TOs are well developed and very large in the Curetinae, but, as already noted by Viehmeyer (1910a), their homology to the TOs of the Lycaeninae seems questionable. They are different not only in function (*Curetis* larvae evert their TOs in response to tactile disturbance and hereby try to ward off potential enemies: Fiedler & Maschwitz, unpublished), but also in location (medioposterior of the spiracle in Curetinae, lateroposterior of the spiracle in Lycaeninae). Thus, the TOs of *Curetis* are most likely the result of convergent evolution (Eliot, pers. comm.), as it is the case with the TOs of Riodinidae (DeVries 1990) and, probably, *Aslauga* (see above).

Looking now back on the 3 lycaenid subfamilies Poritiinae, Miletinae, and Curetinae, the following generalizations are possible:

1.) PCOs are widespread, if not ubiquitous, but, as in the Riodinidae, there is no evidence that these organs are attractive to ants.
2.) A DNO is always absent. There is no plausible morphological or functional indication for a homology between the epidermal grooves of *Allotinus* and *Curetis* and the true DNO of the Lycaeninae.
3.) TOs are present only in two isolated genera (*Curetis, Aslauga*), and it is very likely that these structures evolved independently of the TOs of the Lycaeninae. The general potential to develop eversible epidermal structures is obviously an ancestral character of the whole Riodinidae-Lycaenidae group.

Thus, neither the comparative study of the larval and pupal morphology of the Lycaenidae subfamilies retaining a number of plesiomorphic characters, nor the comparisons with Nymphalidae and Riodinidae as outgroups lend support to the idea of ancestral myrmecophily. Instead, the ancestral lycaenids apparently had primarily myrmecoxenous caterpillars, and only a small fraction of them evolved myrmecophilous life-habits as carnivorous or ant-parasitic species (Miletinae), or perhaps as commensales (Poritiinae, see below). The "typical" myrmecophily of lycaenid caterpillars is restricted to the largest subfamily Lycaeninae.

Myrmecophilous organs of the Lycaeninae

The larvae within this subfamily primarily bear a full set of ant-organs (PCOs, a DNO and TOs), and they are generally myrmecophilous. In fact, the true DNO is confined to this subfamily and represents one of its most important synapomorphies.

The Aphnaeini are now generally accepted as the earliest offshoot from the Lycaeninae, and in nearly all known Aphnaeini larvae this equipment has been retained. Only in some species of *Aloeides* and in the small genus *Phasis* the DNO is reduced, at least in the final instar (Clark & Dickson 1971, Henning 1983a). On the other hand, some species (*Spindasis, Crudaria leroma*) possess further, presumably glandular structures ("dish organs": Clark & Dickson 1971, Cottrell 1984) that are highly attractive to ants. The TOs of the specialized "whip type" are always well developed from the first instar on (Clark & Dickson 1956).

Caterpillars of the tribe Lycaenini all lack the DNO and TOs, but possess PCOs. Many Lycaenini pupae and the larvae of at least four North American *Lycaena* species additionally possess dendritic setae that seem to be related to myrmecophily (Ballmer & Pratt 1988 and in press). Typically, Lycaenini larvae are myrmecoxenous, this trait most likely being a case of secondary reduction.

It is, however, not yet clear from which lycaenid group this reduction had started. Three hypotheses exist that are all supported by some evidence.

— The Lycaenini may have branched off from the Lycaeninae stem as the second group after the Aphnaeini (this possibility is in accordance with the similarities between Aphnaeini and Lycaenini in external appearance as well as with the apparent early origin of the Lycaenini as indicated by their zoogeography).
— Or the Lycaenini may be the sister-group to, or even a specialized, but early offshoot from the Polyommatini (Eliot, pers. comm.).
— Or the Lycaenini may be the sister-group of the Eumaeini +Polyommatini (based on some characters of first instar larvae: Scott & Wright 1990).

Irrespective of the detailed phylogeny of this tribe, it is important to note that myrmecoxeny is probably a secondary character of Lycaenini larvae, whereas in the Riodinidae subfamilies Hamearinae and Euselasiinae, and the lycaenid subfamilies Poritiinae, Miletinae, and Curetinae, myrmecoxeny is a primary character state. Alternatively, one would have to assume that the Lycaenini are the sister-group of the remaining Lycaeninae tribes, or that the DNO of Aphnaeini and of the tribes Theclini, Eumaeini and Polyommatini have evolved in parallel. For both these ideas there is at present no support.

The majority of Theclini larvae possess the full complement of myrmecophilous organs. The TOs of Theclini, Eumaeini and Polyommatini, however, are always smaller than those of the Aphnaeini ("beacon type" of Clark & Dickson 1956). Reductions repeatedly occur in several groups.

At least some species of the Luciiti genus *Philiris* have neither a DNO nor TOs (Ballmer & Pratt 1988), while others have apparently retained the DNO at least (Parsons 1984). The TOs are likewise lost in the genus *Acrodipsas* whose larvae permanently live inside ant-nests (Samson 1989).

The second Theclini subtribe with reduced myrmecophilous organs are the Thecliti. In this group the TOs are entirely missing, and the presence of the DNO has not yet been confirmed without doubt (e.g. Malicky 1969b). The only Thecliti species with all ant-organs present is the systematically isolated *Amblopala avidiena* (Uchida 1985).

Eumaeini larvae are basically myrmecophilous, as well, and they bear all types of ant-organs. This situation is largely retained in the subtribes Catapaecilmatiti, Amblypodiiti and Loxuriti. However, reductions of the myrmecophilous organs and secondary myrmecoxeny are widespread among the Eumaeini.

In the subtribe Iolaiti records of ant-associations are scattered. At least some Iolaiti species are suspected to have a reduced set of ant-organs (Farquharson 1922; but see Clark & Dickson 1971). In the Deudorigiti, certain endophytic species have lost the

TOs, and some have even reduced the DNO. The most pronounced tendency to reduce ant-associations is found in the Eumaeiti. No Eumaeiti larva is known to possess TOs, and the DNO is sometimes reduced to a non-functional rudiment (e.g. some *Callophrys* and *Satyrium* species: Malicky 1969b, Fiedler 1990d), or even completely lost in a number of species (e.g. *Eumaeus* spp., *Satyrium pruni, Erora* spp., see Appendix).

Polyommatini caterpillars usually possess all types of myrmecophilous organs and are associated with ants. Reductions of the TOs occur in several endophytic genera (*Cacyreus, Harpendyreus, Cupido*) and in those species living inside ant-nests (*Maculinea, Lepidochrysops*), while total reductions of both DNO and TOs are rare (*Cacyreus, Udara blackburni, Plebejus optilete*, subgenus *Agriades* of *Polyommatus*; see Appendix).

The higher lycaenid taxa and their ant-associations

Poritiinae

The only Poritiini species whose larval biology is known (*Poritia erycinoides*) has hairy caterpillars that live gregariously on Fagaceae trees without being ant-attended (Rosier 1951).

Liptenini larvae are extremely hairy as well, but feed on lichen and similar substrates. Ant-associations are entirely unknown from Pentiliti and Durbaniiti, while the larvae of some Lipteniti genera (*Liptena, Teratoneura, Deloneura, Epitola, Hewitsonia*) appear to be mostly found on trees occupied by *Crematogaster* ants (Farquharson 1922, Jackson 1937, Ackery & Rajan 1990). However, direct caterpillar-ant interactions have rarely been reported, and Farquharson (1922) observed that the ants always avoided contacts with the fuzzy caterpillars of *Teratoneura isabellae*. Thus, the relationship between these Lipteniti larvae and ants is co-existence (or perhaps commensalism in a few cases) rather than myrmecophily in a more sophisticated sense.

Anyway, the Poritiinae are one of the lycaenid groups where the knowledge of larval biology is distinctly insufficient, and the description of further life-histories almost certainly will modify the current picture.

Miletinae

Miletinae larvae are carnivorous or feed on excretions of Homoptera or trophallactic regurgitations of ants (Cottrell 1984).

Within the Miletini, caterpillars of the least specialized subtribes Spalgiti and Tarakiti (*Spalgis, Feniseca, Taraka*) feed on ant-tended coccids, but are not always tolerated by the ants. As protective device they either feed inside silken shelters (*Feniseca, Taraka*), or they cover themselves with the remains of their prey (*Spalgis*). Thus, Spalgiti and Tarakiti larvae are not truly myrmecophilous. The caterpillars of the Miletiti, in contrast, are usually fully tolerated, but largely ignored within the trophobiotic ant-Homoptera associations (*Logania, Allotinus, Miletus, Megalopalpus*).

At least some Miletiti species have in fact close relationships to ants, either using ants as oviposition cues (*Allotinus unicolor, Miletus* spp.: Maschwitz et al. 1988, Fiedler & Maschwitz 1989c) or even living and pupating inside ant nests (*Allotinus apries, Miletus* spp.: Cottrell 1984, Maschwitz et al. 1988).

Even closer ant-associations occur in the Lachnocnemiti. *Lachnocnema bibulus* larvae have been observed to be carried into *Camponotus* nests (Cripps & Jackson 1940), and the caterpillars of at least some *Thestor* species live and pupate inside *Anoplolepis* nests (Clark & Dickson 1971).

The second Miletinae tribe Liphyrini, then, is highly adapted to live in association with ants. *Aslauga* larvae feed on Homoptera and are ignored by ants (as with *Allotinus*), while *Liphyra* and *Euliphyra* are specialized predators or parasites in *Oecophylla* nests.

In all, Miletinae caterpillars are well adapted to avoid ant-attacks when preying upon the ants' trophobionts, but true myrmecophily has been evolved independently only in some advanced groups, and all these myrmecophiles are detrimental to their ant hosts. The systematic distribution of myrmecophily within the Miletinae indicates an evolutionary sequence from loose and incidental associations, over consistently tolerated "guests" in trophobiotic associations, up to highly adapted inquilines.

Curetinae

Curetis larvae are usually not ant-associated (Hinton 1951, Iwase 1954, Eliot 1980). DeVries (1984) found larvae of *C. regula* visited by ants (*Anoplolepis longipes*), but these ants were mostly attracted to the sap-flow caused by the larval feeding activities and largely ignored the caterpillars themselves.

Own observations with *C. felderi* revealed that the larvae are not attractive to ants (*Anoplolepis, Oecophylla, Pheidole*) and, in particular, do not release the typical palpation behaviour. One *Crematogaster* species even severely attacked a caterpillar. When observed on the natural hostplant without disturbance, *C. felderi* larvae were ignored by *A. longipes* that attended the extrafloral nectaries of the hostplant. The TOs were never seen everted unless a caterpillar was prodded (using a blade of grass), or was attacked by *Crematogaster* ants. The latter were not repelled by repeated TO eversions (Fiedler & Maschwitz, unpublished). In summary, the current evidence indicates that Curetinae larvae are not really myrmecophilous.

Lycaeninae

A p h n a e i n i — All species of this tribe, for which sufficient life-history information is present, are at least facultatively associated with ants. In the majority of cases their myrmecophilous relationships appear to be even obligatory and specific.

Larvae of the genera *Aphnaeus, Spindasis, Cigaritis, Crudaria, Phasis, Aloeides* and *Poecilmitis* often rest or diapause in ant nests, and their host ants are in constant attendance. Some caterpillars are known or strongly suspected to be fed by ant-regurgitations (*Spindasis, Cigaritis, Axiocerses*).

In other species the females only oviposit in the presence of the appropriate host ants (e.g. Henning 1983a, b). The myrmicine ant genus *Crematogaster* is the dominant host taxon for Aphnaeini caterpillars, but a few of them have other host ants (*Aloeides, Erikssonia: Acantholepis; Poecilmitis pyroeis: Camponotus*).

Some species in the genera *Spindasis* and *Cigaritis* apparently are commensales in ant nests (Hinton 1951, Larsen & Pittaway 1982), and the larvae of the genera *Tylopaedia, Trimenia, Argyrocupha*, and *Oxychaeta* are strongly suspected to be entirely aphytophagous, probably living as brood predators inside ant nests (Clark & Dickson 1971, Cottrell 1984).

As a whole, the Aphnaeini are the lycaenid tribe with the most intimate and specific relationships towards ants, and no single case of secondary myrmecoxeny is known from that group.

Lycaenini — Ant-associations are rare in this tribe, suggesting that the larvae of the copper butterflies are usually myrmecoxenous. Their PCOs are attractive to ants, but this attractiveness is normally not sufficient to induce stable ant-associations (see above).

Old records of ant-associations are available for the Palaearctic *Lycaena dispar* (Hinton 1951), but require confirmation, since in the extensive recent literature about this locally endangered species no such associations are mentioned (e.g. Duffy 1968, but see Ebert & Rennwald 1991).

The four North American species with myrmecophilous larvae bearing dendritic setae (*Lycaena rubidus, xanthoides, editha* and *heteronea*) have already been mentioned (Ballmer & Pratt 1988, and in press). The presence of dendritic setae in the larvae of these four species must be regarded as an apomorphic character state, and thus their ant-associations may represent a kind of “tertiary myrmecophily” within the Lycaenini. Females of *L. rubidus* have been observed to oviposit in association with *Formica* ants (Funk 1975, Pierce, pers. comm.), and a closer investigation of this phenomenon seems worthwhile.

Theclini — Judging from the widespread records of ant-associations, Theclini caterpillars are generally myrmecophilous, although information regarding the two most species-rich subtribes Luciiti and Arhopaliti is still very scanty.

A number of Luciiti species (*Lucia, Paralucia*, and partly *Hypochrysops*) are obligatorily associated with specific host ants (Common & Waterhouse 1981, Sands 1986), and the *Acrodipsas* species even live as brood predators inside ant nests throughout their whole larval period (Samson 1989). Reductions of myrmecophily occur in the genus *Philiris* (Parsons 1984, Wood 1984).

The Ogyriti, Zesiiti and Arhopaliti are entirely myrmecophilous, as far as is known today, again with numerous obligatory ant-caterpillar relationships.

The Thecliti larvae, however, with their ant-organs reduced (see above), largely lack ant-associations (Iwase 1954, Shirôzu 1962). The only well documented myrmecophile in this subtribe is *Shirozua jonasi* whose larvae feed on aphids, their honeydew, and

regurgitations of the specific host ant *Lasius spathepus* (Cottrell 1984). In general, the Theclini can be described as a distinctly myrmecophilous taxon with reductions restricted to only two lineages.

Eumaeini — Ant-associations are widely distributed among this tribe, but reductions of ant-organs and myrmecophily are common in several of its subgroups.

The larvae of the subtribes Catapaecilmatiti, Amblypodiiti, Loxuriti and Iolaiti are generally myrmecophilous, but secondary myrmecoxeny is known from *Cheritra freija*. Judging from the scanty records the level of myrmecophily is generally low within the Iolaiti. No ant-associations have hitherto been reported for *Amblypodia anita* and numerous Iolaiti species, despite the presence of a DNO and TOs in most of them.

The Remelaniti and Hypolycaeniti are myrmecophilous, but TOs are only doubtfully recorded for *Ancema blanka* and two species of *Hypolycaena* (*H. lebona, H. othona*). TOs may in fact be missing in both groups. Two other species (*H. erylus, H. phorbas*) are the only well-documented examples of obligatory myrmecophily in the entire tribe Eumaeini with its more than 1500 species. Nothing is known about ant-associations in the subtribes Hypothecliti and Oxyliditi.

Myrmecophily has been reported from numerous Deudorigiti species, but reductions of ant-organs are not rare, especially among the species with larvae boring in flowers or fruits, where ants have limited access. The TOs, in particular, are missing in most species of the genus *Deudorix* s. l. and in *Capys*, whereas the genera *Rapala* and *Tomares* have retained their full complement of ant-organs and are facultatively myrmecophilous.

The largest subtribe Eumaeiti, which is undoubtedly closely related to the Deudorigiti, exhibits even more pronounced tendencies towards reductions of myrmecophily which closely parallel the reductions of ant-organs within this group (see above). None of the more than 1000 Eumaeiti species is yet known to be obligatorily myrmecophilous, and ant-associations have been definitely reported for only 27 of the 221 species where life-history information is available. As in the Deudorigiti, many species have endophytic fruit-boring larvae.

Polyommatini — Myrmecophily occurs nearly universally among Polyommatini caterpillars with only very few secondary exceptions. In the subtribe Candaliditi one species is stated to be myrmecoxenous (*Candalides albosericea*: Common & Waterhouse 1981), but no ecological and morphological details are given there.

The Lycaenesthiti are likewise ant-associated, and some species are known to be even obligate myrmecophiles. Two species were reported by Jackson (1937) to be myrmecoxenous, but this statement should be taken with caution on the following reasoning. Jackson, whose life-history reports are extremely accurate in other respects, stated that he could not find myrmecophilous organs on the larvae of four *Iolaus* and three *Anthene* species, but the painstaking studies by Clark & Dickson (1971) and Henning (e.g. 1983a) clearly confirmed the presence of all ant-organs in several closely related species.

Obviously, Jackson's optical equipment precluded a final decision in such species where the ant-organs are small or only occasionally extruded.

The life-history of only one species of the small subtribe Niphanditi has been recorded, this caterpillar being an obligate myrmecophile of *Camponotus* ants.

Well documented cases of secondary myrmecoxeny occur scatteredly in the Polyommatiti (*Uranothauma, Cacyreus, Udara blackburni, Plebejus optilete*, subgenus *Agriades* within *Polyommatus*). These are, however, rare exceptions that are by far outnumbered by the numerous obligatory ant-associations in the genera *Maculinea, Lepidochrysops*, and possibly *Tarucus* and *Plebejus*.

Viewing now back on the Lycaenidae as a whole, it becomes apparent that trophobiotic caterpillar-ant interactions are restricted to the subfamily Lycaeninae, due to the possession of the DNO as a keystone synapomorphy. However, within this subfamily myrmecophily is widespread and prevalent, the associations covering the entire range of ant-caterpillar interactions, from facultative or obligate trophobiosis to predatory parasitism, possibly commensalism, and simple coexistence.

The Lycaeninae tribes and subtribes usually exhibit characteristic levels of myrmecophily. Very close and often obligate ant-associations have mainly evolved in the Aphnaeini, Theclini, and in some Polyommatini. On the other hand, reductions of ant-organs and ant-associations have occurred in all tribes except the Aphnaeini, but secondary myrmecoxeny is typical only for the Lycaenini and Thecliti, and is rather widespread among the Deudorigiti and Eumaeiti.

The preceding two paragraphs gave a very condensed survey over the morphology and ecology of lycaenid caterpillars with respect to myrmecophily. Many details and references compiled in the tables (see Appendix) were omitted here, and all discussions were restricted to subfamilies, tribes, and subtribes.

Anyway, a generalized pattern becomes apparent, i.e. the major subtaxa of the family Lycaenidae have characteristic equipments with ant-organs as well as characteristic states of myrmecophily. This general pattern continues on the level of genus-groups ("sections") and genera, indicating that the evolution of myrmecophily is intimately correlated with the phylogeny of the lycaenid lineages.

In fact, on the grounds of this reasoning, any discussions on the evolutionary biology of lycaenid myrmecophily have to take into account such phyletic characteristics and trends. For example: a lycaenid group whose *Bauplan* does not include a DNO (e.g. Poritiinae, Miletinae) can never contain a species maintaining a trophobiotic relationship towards ants as so many Lycaeninae species do, unless within that group a convergent evolution of a trophobiotic gland would take place (as is the case with the myrmecophilous Riodininae tribes).

This conclusion is in marked contrast to the view of Pierce & Elgar (1985) and Pierce (1987: p.107) who stated that "the distribution of ant association within the Lycaenidae is independent of phylogeny". In fact it appears that myrmecophily remains a rather stable character in many lycaenid lineages.

This contrasts well with the trophobiotic associations of Homoptera and ants, that are often compared with lycaenid myrmecophily. In aphids, symbioses with ants have evolved several times in parallel, and ant-association is an evolutionarily rather labile trait (Bristow 1990). However, ant-homopteran mutualisms are based on excretions of superfluous carbohydrates, and these excretions provide a permanently available raw material for the evolution of complex interactions.

In lycaenid caterpillars, specialized glands are required that, once being evolved, were rather firmly incorporated into the morphological groundplan of their caterpillars. Accordingly, as already emphasized by Pierce (1987), ecological or evolutionary comparisons of interactions between ants and caterpillars or homopterans should always bear in mind the principal peculiarities of, and differences between, these organisms.

The pattern outlined here is far from being complete. Continuous recording of life-history information is necessary, especially in those groups where the knowledge is still very fragmentary (Poritiinae, Eumaeiti). Progress in the phylogenetic systematics of the Lycaenidae and their outgroups, as well, will certainly bring about new aspects and facets.

Nevertheless, based on this newly recognized systematic pattern and the life-history information compiled in the Appendix, it seems justified to critically re-examine some hypotheses concerning the specificity of lycaenid-ant interactions, the relations between hostplant choice and myrmecophily, and the biogeography of lycaenid myrmecophily in the following three main chapters. The final section will then consider some aspects of the evolutionary processes leading to, and modifying the ant-associations of the Lycaenidae.

SPECIFICITY OF LYCAENID-ANT INTERACTIONS

Which ants do visit lycaenid caterpillars?

Two general trends are found among the large number of myrmecophiles within the Arthropoda: ant species forming large and long-lived colonies are the preferred hosts of myrmecophiles, and most myrmecophiles are host-specific, i.e. they are associated with one ant species or genus only, or with a small group of ant host taxa (see Kistner 1982 and Hölldobler & Wilson 1990 for extensive reviews).

Both trends are easily understood: large ant colonies provide a significant and sufficiently stable resource in terms of food or shelter; and since ants are usually aggressive against any foreign intruders, specific mechanisms are required to overcome this aggressiveness and successfully enter into an ant society.

The majority of myrmecophiles, however, live inside ant nests at least during one part of their life-cycle and thus differ from the Lycaenidae, where most ant-associations occur outside ant nests on the appropriate larval hostplants. Ant-associations of lycaenid caterpillars in this respect largely parallel the myrmecophily of homopterans, and most trophobiotic associations of ants and homopterans are believed to be facultative or at least unspecific. There is, however, a growing body of evidence that homopterans may gain differential benefits from being attended by specific ants (Bristow 1984).

In addition, amazing specializations of trophobiotic systems have been discovered (e.g. Maschwitz & Hänel 1985). It is hence an interesting question whether the above rules regarding myrmecophily apply to the lycaenids as well.

The problem of specificity of lycaenid-ant interactions has previously been discussed by three authorities. Malicky (1969b), on the grounds of his extensive experimental work and compilation of literature data, concluded that most instances of lycaenid myrmecophily are rather unspecific. He found that most ants responded in largely the same way to a variety of lycaenid caterpillars tested by him. Only ants with special feeding habits (strictly predatory species, seed harvesters, social parasites) never formed associations with larvae.

According to Malicky, the main factor deciding which ants attend which lycaenids in nature is the structure of the ant fauna in the respective microhabitat. Hence, lycaenid larvae living in a given stratum are visited by ants sharing the same niche, and dominant ant species are more likely to be found attending caterpillars than subdominant ant species.

As a consequence, Malicky (1969b) suggested that most cases of lycaenid myrmecophily are unspecific and facultative. Specific relationships were only accepted by him for parasitic species such as *Maculinea*, and he also suspected that among the tropical lycaenids a further number of specific and obligate ant-associations should occur. At that time the knowledge of most tropical taxa was too scanty to allow a more precise assessment.

Cottrell (1984), in his extraordinarily complete review paper, broadly followed this argumentation. However, having compiled data for a larger number of tropical species, he concluded that specific associations occur not only with most lycaenids living within ant nests, but also with a number of species that are obligatorily associated with ants outside their nests in a mutualistic way. Cottrell also discussed possible mechanisms of host-specificity (ant-dependent oviposition, adoption, resource partitioning), but he deferred from the formulation of generalizations since the examples known to him appeared not to be sufficiently worked out.

Recently the hypothesis that the majority of caterpillar-ant interactions are unspecific and facultative received support from a study of DeVries (1991) on myrmecophilous riodinids.

Pierce & Elgar (1985) adopted a totally different view. Based on studies of Australian lycaenids (notably *Jalmenus evagoras*) and a survey of selected literature they concluded that obligatory and specific cases of myrmecophily are rather common among lycaenids in tropical and subtropical regions. In particular, ant-dependent oviposition was assumed to play an important role.

Later on, Pierce (1987) even concluded on the grounds of her literature data that obligate and specific ant-associations are the rule in the southern hemisphere (Australia, India, and southern Africa), while facultative and unspecific associations dominate in the Holarctic region.

However, since the selection of literature data in the papers of Pierce & Elgar (1985) and Pierce (1987) is incomplete and contains a number of doubtful points, the controversy about specificity in lycaenid myrmecophily merits reinvestigation using the broad database given in the Appendix. As a first step, the ants involved in interactions with lycaenids shall be reviewed.

A detailed listing of all cases of lycaenid myrmecophily where the ants involved were determined at least to generic level (field records only) is given in the Appendix (Tab.19). The following Tab.4 gives a condensed overview of how many lycaenid species have been observed associated with each ant genus (limitations of genera following Hölldobler & Wilson 1990). In this latter table, only truly myrmecophilous interactions have been considered. Accordingly, cases where the ants behaved indifferently, or only attended the homopteran food (several Miletinae), were omitted.

When interpreting these tables, one has to be aware of several constraints:

1). In many cases the ants attending lycaenid immatures have not been specified at all.

2). There are undoubtedly misidentifications. Such may be common in taxonomically difficult ant genera where the recognition of sibling species still continues even in well surveyed regions like Europe (e.g. *Myrmica, Lasius*: Seifert 1988 and pers. comm.), whereas the ant genera in most cases should have been determined correctly. However, some doubtful genus records (e.g. *Cataglyphis bicolor* with *Cigaritis myrmecophila*) are omitted from Tab.4.

3). Each ant genus is considered only once for each lycaenid species irrespective of the fact that in a number of cases several ant species of one genus attend the same caterpillar species.

4). The decision whether or not an ant-lycaenid relationship is obligatory, remains uncertain in many cases. Hence, this table gives nothing more than an impression of the diversity of "lycaenophilous" ant genera and their approximate relative importance.

Tab.4: Numbers of Lycaenidae species observed in association with 38 ant genera (field records only). Detailed records see Appendix (Tab.19).

Ant genus	associated lycaenid species	obligate associations
Ponerinae:		
Ectatomma	2	0
Rhytidoponera	1	0
Odontomachus	1	0
Myrmicinae:		
Myrmica	22	6
Pheidole	28	4
Myrmicaria	2	1
Crematogaster	89	41
Monomorium	7	0
Solenopsis	1	0
Meranoplus	1	0
Tetramorium	4	0
Cataulacus	1	0
Dolichoderinae:		
Dolichoderus	6	4
Hypoclinea	1	1
Monacis	1	0
Azteca	1	0
Iridomyrmex	42	20
Tapinoma	21	0
Conomyrma	2	0
Dorymyrmex	2	0
Forelius	1	0
Froggatella	4	1
Technomyrmex	5	0
Engramma	1	0
Formicinae:		
Oecophylla	16	8
Notoncus	3	1
Prolasius	1	0
Acantholepis	6	4
Anoplolepis	10	5?
Plagiolepis	10	0
Brachymyrmex	1	0
Prenolepis	6	0
Paratrechina	3	0
Lasius	27	2
Myrmecocystus	1	0
Formica	33	1
Camponotus	48	15
Polyrhachis	3	0

Several conclusions can be drawn from this table:

1.) Only ant genera that normally exhibit trophobiosis are involved in lycaenid myrmecophily, confirming the findings of Malicky (1969b) and DeVries (1991). The 38 genera documented represent about 12.8 % of the whole generic diversity of the Formicidae (297 genera according to Hölldobler & Wilson 1990), i.e. considerably more than the 20 genera mentioned by DeVries (1991) for Riodinidae and Lycaenidae together.

Strictly predatory ants as most Ponerinae and members of the subfamilies Ecitoninae, Dorylinae, and Leptanillinae never associate with lycaenids, neither do harvester ants (*Pogonomyrmex, Messor* etc.), fungus growers (*Atta*), slave raiders (*Polyergus*), or social parasites.

Four subfamilies have not yet been found associated with lycaenids (i.e. Nothomyrmeciinae, Myrmeciinae, Aneuretinae, and Pseudomyrmecinae), although these are known to collect honeydew or plant nectar.

At least from the Pseudomyrmecinae true trophobiosis is documented (e.g. *Tetraponera*; see Klein 1990), and it seems feasible that associations of lycaenids with members of this subfamily will be detected in the course of future research.

2.) *Crematogaster, Pheidole, Iridomyrmex*, and *Camponotus* are the most species-rich and dominant trophobiotic ant genera on a worldwide scale, and they are the most important partners for lycaenids as well.

The high figures for *Myrmica, Formica*, and *Lasius* are influenced by an "Holarctic bias": these three genera are abundant and often dominant trophobiotic ants in Europe and North America, and since these two regions are best known with regard to lycaenid biology, the high number of records for them is not surprising.

With increasing knowledge of tropical lycaenids, the relative quantitative importance of these three genera should decrease. *Oecophylla*, despite being a very small genus with only two species, is important for lycaenids as well, and this is due to its ecological dominance in many of its habitats. These results are confident with the findings of Malicky (1969b) and DeVries (1991) that dominant trophobiotic ants preponderate in lycaenid-ant interactions.

3.) Obligate lycaenid myrmecophily is only known from 14 ant genera (38.9 % of the 36 genera involved), and only 114 of the 411 lycaenid species (27.8 %) considered in Tab.4 are obligatorily myrmecophilous. These figures are rather difficult to explain. The proportion of obligatorily myrmecophilous lycaenids is almost certainly an overestimate, as will be discussed later.

Ant genera that form large and long-lived societies (e.g. *Crematogaster, Iridomyrmex, Oecophylla*) have the greatest numbers of obligatorily myrmecophilous lycaenids, thus repeating the general pattern known from other myrmecophiles. There are, however, differences among the ant genera that might be important. *Myrmica, Lasius* and *Formica*, for example, have few obligate myrmecophiles among the Lycaenidae. In genera such as *Camponotus, Oecophylla, Crematogaster*, and *Iridomyrmex* about one third to one half of the associated lycaenids are obligate myrmecophiles.

Dolichoderus and *Hypoclinea*, in contrast, have almost exclusively been observed with specific myrmecophiles. Furthermore, records of ant-associations are astonishingly sparse for these two highly trophobiotic genera, suggesting that lycaenids can only maintain associations when specializing towards such hosts using very peculiar mechanisms. Interestingly, *Dolichoderus* and *Hypoclinea* are among the ant genera with the most extreme specializations towards trophobiosis (obligate symbiosis with specific homopterans, true nomadism: Maschwitz & Hänel 1985, Dill 1990).

One should, however, keep in mind that the decision whether or not a given lycaenid is an obligate myrmecophile, is in many cases not yet sufficiently established. Furthermore, ant-associations of lycaenid caterpillars are far more conspicuous, and hence more likely to be reported, if these associations are close and permanent or if the larvae even live inside ant nests.

When lycaenid larvae are only occasionally visited by ants, myrmecophily is more likely to be overlooked. Therefore, the data presented in Tables 4 and 19 are probably biased towards too a high proportion of obligate myrmecophily for both the ant genera and lycaenid species.

4.) In the Polyommatini, at least, several species have a wide range of attendant ants, in some cases 10 or 11 ant species from 3 subfamilies (Myrmicinae, Dolichoderinae, Formicinae). Similar evidence was obtained in laboratory experiments by Malicky (1969b).

Furthermore, in own laboratory trials *Camponotus floridanus* from Florida and a Malaysian *Crematogaster* species attended fourth instar larvae of the Palaearctic *Polyommatus icarus* in the usual way, whereas *Pseudomyrmex mexicanus* from Florida totally ignored caterpillars of the same species without any signs of aggressiveness (Fiedler, unpublished).

These findings indicate that in facultatively myrmecophilous lycaenids the signals the larvae emit are so generalized that nearly any trophobiotic ant species, even from different zoogeographic regions than the caterpillars, may respond adequately to the latter.

Mechanisms of host-specificity

Basically there are two different, but not mutually exclusive possibilities as to how specific lycaenid-ant associations can be founded: either the females select the appropriate host ants for oviposition, or the caterpillars communicate selectively with certain ant species.

The former mechanism (ant-dependent oviposition) was first conclusively demonstrated by Atsatt (1981b) for the Australian *Ogyris amaryllis* and was later on confirmed for *Jalmenus evagoras* by Pierce & Elgar (1985) and Smiley et al. (1988). Pierce & Elgar (1985) provided evidence from the literature that the use of ants as oviposition cues for females of myrmecophilous lycaenids might be widespread.

Their database, however, contains a few inaccuracies:

1). There are some taxonomic errors and misspellings of names (e.g. *Lepidochrysops quassi* assigned to the genus *Catochrysops* [as *phasma*], *Leptotes plinius* assigned to *Tarucus (Castalius)*, i.e. in both cases to unrelated genera).

2.) The claimed specificity of associated ants is not as distinct for *Lachnocnema bibulus* (recorded with *Pheidole, Crematogaster* and *Camponotus*), *Spindasis vulcanus* (recorded with *Crematogaster* and *Pheidole*), *Ogyris amaryllis* (recorded with *Iridomyrmex, Camponotus*, and *Crematogaster*), and *Chilades trochylus* (recorded with *Pheidole, Iridomyrmex*, and *Prenolepis*).

3). Older larvae of *Lycaena rubidus* and, especially, *Chilades trochylus* are steadily associated with ants, contradictory to the statement of Pierce & Elgar.

4). Oviposition substrates and larval hostplants have been confused several times (e.g. for carnivorous Miletinae whose larvae never feed on plants: *Megalopalpus zymna, Lachnocnema bibulus*).

A critical evaluation of the far more complete compilation of literature records given in the Appendix reveals that evidence for ant-dependent oviposition (though often only indirect or anecdotal) is now present for at least 56 species from 27 genera. In extreme cases oviposition may occur on plants that are totally unacceptable for larval nutrition, if only the appropriate host ants are present (e.g. *Anthene emolus* among *Oecophylla* ants on Zingiberaceae: Fiedler, pers. observ.; *Plebejus argus* on bracken, *Pteridium aquilinum*: Mendel & Parsons 1987), but mostly the combination of both hostplants and ants is required.

Detailed investigations of the physiological mechanisms involved in host ant recognition are lacking, but from behavioural observations it can be concluded that visual stimuli are likely to be used in the detection of ant assemblages at a greater range, while the specific recognition is probably mediated by olfactory stimuli at a close range (e.g. Pierce & Elgar 1985, Fiedler & Maschwitz 1989b, c).

Ant nests or trails, or ant-homopteran associations certainly provide sufficient visual cues to be detected by lycaenid females, and the olfactory distinction between various ants based on the diversity of ant pheromones seems feasible, given the excellent ability of most butterfly species to respond specifically to chemical cues of their hostplants.

Observations on species of the genera *Poecilmitis, Aloeides, Erikssonia* and *Anthene* in fact indicate that the females, after having landed near an ant trail, intensively investigate the substrate with the antennae and fore tarsi before oviposition commences (Henning 1983a, 1984, Fiedler & Maschwitz 1989b).

Although ant-dependent oviposition seems not to be a rare curiosity among the Lycaenidae, it has yet been documented almost exclusively in obligately myrmecophilous species (but see the report of Funk 1975 that ovipositing female *Lycaena rubidus* are associated with *Formica altipetens*).

In obligate myrmecophiles ant-dependent oviposition secures the attendance of, or adoption by, appropriate host ants from the beginning of the larval period. Facultatively myrmecophilous lycaenids are almost unknown to show such behaviour, and some

of the records cited in the work of Pierce & Elgar (1985) must be taken with caution (see above). Hence, ant-dependent oviposition is likely to be of more restricted importance than suggested by these authors.

The second way to found specific ant-associations, selective communication of the larvae with its host ants, appears to be less advantageous at the first glance. There is, however, a growing body of evidence that such communication does occur.

As can be seen from the experimental data on larval attractiveness (Malicky 1969b, Ballmer & Pratt in press, this work), different ant species react differentially towards lycaenid caterpillars. This might allow a first step towards specific ant-associations in the course of ecological time: ants stay only with larvae whose secretions are sufficiently attractive.

Lanza & Krauss (1984) and Lanza (1988) demonstrated that different ant genera selectively prefer specific concentration profiles of carbohydrates, amino acids, or peptides in artificial nectars, and the observations of Pierce (1989) strongly indicate that some Australian *Jalmenus* species make use of such specificities. The secretions of these lycaenids differ importantly in their amino acid profiles, and the specific host ants are most strongly attracted by the secretions of "their" appropriate lycaenid trophobionts.

The TOs offer another example of specific reactions of ants towards lycaenid caterpillars, as these organs activate only a part of the large guild of potential trophobiotic ant partners (see above).

However, there is a strong selective disadvantage that all these specificities only gain importance after a caterpillar has been detected by ants. Accordingly, a number of caterpillars might be found by inadequate or even hostile ants. In the case of specific and obligate associations, at least, one would therefore expect that the caterpillars themselves might have evolved mechanisms to locate their host ants. Surprisingly, evidence for this is very incomplete.

Observations on several African Aphnaeini (*Poecilmitis lycegenes, Aloeides dentatis, A. thyra, Erikssonia trimeni, Cigaritis zohra*; Claassens & Dickson 1977, Henning 1983a, 1984, Rojo de la Paz 1990) suggest that these caterpillars follow the pheromone trails of their host ants, but clear experimental evidence is lacking.

Furthermore, the possibility that these caterpillars use their own trail pheromones has not yet been ruled out. The physiological potential for trail-following (and trail-laying) is likely to be present in the Lycaenidae, since both behaviours are known from several Lepidoptera larvae (Lasiocampidae: Weyh & Maschwitz 1978, Peterson 1988; Saturniidae: Capinera 1980; Yponomeutidae: Roessingh et al. 1988), including butterflies (Nymphalidae: Bush 1969; Papilionidae: Weyh & Maschwitz 1982).

Rojo de la Paz (pers. comm.) indeed observed that larvae of *Cigaritis zohra* produce silk trails between the nests of *Crematogaster laestrygon* (wherein they rest during daytime) and their feeding places, and these trails appear to serve as guiding structures. Thus, orientation along ant chemicals may only be used in this species at the very first locating of the ant nest, whereas later caterpillar trails may be used.

In fact, the ant-associations of the above mentioned Aphnaeini species are all first established via ant-dependent oviposition, and trail-following and/or other means of specific chemical communication between caterpillars and ants (e.g. with the TOs) only enhance and stabilize the associations later on. In another very close ant-lycaenid association (*Anthene emolus/Oecophylla smaragdina*) no indication of trail-following by the larvae was obtained (Fiedler & Maschwitz 1989b).

Hence, there seems to exist a general pattern that specific caterpillar-ant association are usually established via ant-dependent oviposition, whereas specific communication between caterpillars and ants, although potentially rather widespread, is less suitable for the foundation of specific and obligate ant-associations within the Lycaenidae. Such communication usually becomes increasingly important after associations have been established.

Two important exceptions from this latter generalization are rather well-known: the genera *Maculinea* and *Lepidochrysops* whose larvae feed on specific hostplants first, but complete their development as predators or parasites in ant nests.

Maculinea larvae leave their hostplants immediately after the moult into the fourth instar and crawl or drop off to the ground. There they wait until they are detected by an ant. Ants of various genera briefly inspect and antennate the larvae, but only *Myrmica* ants intensively palpate them and finally carry them into their nest.

There are significant differences among the *Maculinea* species with regard to the behavioural sequences involved in this adoption process, but usually any *Myrmica* species will adopt the caterpillars of all *Maculinea* species (Thomas et al. 1989, Fiedler 1990b, Elmes et al. 1991a, b; but see Liebig 1989 who reported differential acceptance of *Maculinea alcon* caterpillars by two *Myrmica* species).

There is strong circumstantial evidence that brood pheromone mimics are involved in the adoption of *Maculinea* larvae (Elmes et al. 1991a, b), and the brood odours of *Myrmica* larvae are known to be only genus specific (Brian 1975). However, once arrived in the ant nest, survival of the *Maculinea* caterpillars critically depends on whether or not they have been adopted by an adequate host species of *Myrmica*.

All *Maculinea* species have only a limited number (1—3) of host ant species, and larval mortality is extremely high with inadequate hosts (Thomas et al. 1989, Elmes et al. 1991a, b). The lycaenids, in this case, cannot actively manipulate their chance of being adopted. The findings of Schroth & Maschwitz (1984) that *M. teleius* caterpillars selectively follow *Myrmica* pheromone trails could not be reproduced by Fiedler (1990b). Furthermore, Thomas (1984) and Elmes & Thomas (1987) have observed that *Maculinea* caterpillars always passively await adoption.

Pierce & Elgar (1985) cited old observations of Frohawk indicating that *M. arion* females oviposit in the vicinity of ant nests, but more recent studies of *M. arion, M. teleius*, and *M. nausithous* (Thomas 1984, Elmes & Thomas 1987) could not confirm ant-dependent oviposition.

The only mode how *Maculinea* butterflies can enhance the chance of their offspring being adopted by the right host ants is to stay in the same habitat where they have

developed themselves. In fact, all *Maculinea* species show a tight binding to certain habitats where they usually utilize the most common *Myrmica* species as a host (e.g. *Maculinea arion/Myrmica sabuleti* in dry open grassland with large stands of *Thymus*, *Maculinea nausithous/Myrmica rubra* in moist meadows with *Sanguisorba officinalis*; see Elmes & Thomas 1987, Thomas et al. 1989).

Thus, the establishment of the correct ant-association is a random process in the genus *Maculinea*: the larvae are found by ants only by chance, and it is again a matter of random whether they are adopted by their appropriate hosts.

A system remarkably similar to the *Maculinea/Myrmica* association is that of the African genus *Lepidochrysops* with ants of the genus *Camponotus*. The larvae feed on flowers during the first two instars and are then carried by their host ants into the nests, where they feed on ant brood and regurgitations (Cottrell 1984).

Observations by Cripps (1947) and chemical studies conducted by Henning (1983b) support the hypothesis that mimics of ant-brood pheromones elicit adoption after a typical behavioural sequence. *Lepidochrysops* larvae have never been observed actively entering into ant nests (Claassens 1976).

In most reports of oviposition, no mention is made of ant-dependent hostplant selection (Cottrell 1965, Clark & Dickson 1971, Claassens & Dickson 1980), but Henning (1983b) states that in his laboratory studies the presence of ants was necessary to induce oviposition in *Lepidochrysops ignota*. However, since he obtained very low numbers of eggs, these data are not fully convincing.

In any case, the obligate and specific ant-associations of *Lepidochrysops* larvae are mainly achieved by adoption through the host ants (mediated by pheromone mimics), with ant-dependent oviposition possibly being involved. The larvae again do not actively search their hosts.

Summarizing this chapter, there is strong evidence that ant-dependent oviposition is the main strategy of establishing specific lycaenid-ant associations, while selective communication of the larvae with ants is less important, but does occur. For both mechanisms more detailed studies on a broader range of species are required. In the large number of facultatively myrmecophilous lycaenid species, specific communication plays only a minor, if any role (e.g. ant responses to the TOs).

The obligatory and specific myrmecophiles within the Lycaenidae

Obligate and specific ant-associations are hitherto known or strongly suspected from only a limited number of lycaenid species. The biogeographical distribution of obligate myrmecophily among the Lycaenidae is remarkably uneven (Pierce 1987, and see below), and there is again a strong systematic implication.

In the following, the obligate myrmecophiles are briefly characterized in a systematic arrangement. Obligate ant-associations are unknown from the subfamily Curetinae and from the tribes Poritiini and Lycaenini. Therefore these taxa are omitted here.

Poritiinae

Obligate myrmecophiles are not known from this subfamily with certainty. Observations of Farquharson (1922) and Jackson (1937) indicate that the larvae of some species of the Lipteniti genera *Liptena, Teratoneura, Deloneura, Iridana, Epitola* and *Hewitsonia* only occur on trees infested with *Crematogaster* ants, but direct interactions of these hairy caterpillars with ants have not been reported.

Instead, at least in *Teratoneura isabellae* the ants avoid contacts with the larvae. Possibly some obligate commensalic relationships do exist among the Lipteniti, but this awaits further study.

Miletinae

Obligate myrmecophily is unknown from the Spalgiti and Tarakiti, and is only documented for some Miletiti, Lachnocnemiti and Liphyrini. Five species of *Miletus* have always been found feeding in Homoptera associations tended by *Dolichoderus* ants (old reports of *Polyrhachis* are probably misidentifications), and at least in some cases the females oviposit exclusively when *Dolichoderus* ants are present. However, the caterpillars are largely ignored by the ants, and direct interactions seem to be rare (Eliot 1980, Cottrell 1984, Maschwitz et al. 1985a, 1988).

A similar situation is found in *Allotinus unicolor* where the adults are selectively associated with the ant *Anoplolepis longipes* tending homopterans, while the larvae are again ignored (Maschwitz et al. 1985a, Fiedler & Maschwitz 1989c). The congeneric *A. apries* pupates in ant nests (*Myrmicaria lutea*) and is strongly suspected to live there as a predator from the second instar onwards (Maschwitz et al. 1988).

In the Lachnocnemiti obligate myrmecophily appears to occur in *Thestor*: mature larvae and pupae of several species have exclusively been found in nests of the ant *Anoplolepis custodiens*. Young instars of *Th. basutus* and *Th. protumnus* feed on psyllids or coccids (Clark & Dickson 1971, Migdoll 1988), and the details of the ant-relationships of older *Thestor* larvae remain to be unravelled (predatory on ant brood or on Homoptera in the nests?). Observations on *Lachnocnema bibulus* are controversial. The caterpillars have been found feeding on Homoptera without further attendance of the ants present (Cottrell 1984), but Cripps & Jackson (1940) observed larvae being carried into the nests by *Camponotus* ants; the larvae were even sometimes fed with regurgitations.

In the Liphyrini the caterpillars of *Liphyra* and *Euliphyra* are obligate inhabitants of *Oecophylla* nests where they feed on ant brood (*Liphyra*) or are fed with regurgitations (*Euliphyra*; Hinton 1951, Cottrell 1984, 1987). Oviposition takes place near the host nests. The larvae of the only other Liphyrini genus on which information is available (*Aslauga*) are not truly myrmecophilous, but they are tolerated and ignored when feeding on ant-associated Homoptera.

Lycaeninae

Obligate ant-associations are common among the Aphnaeini. In fact, practically all species of the genera *Aphnaeus, Spindasis, Crudaria, Phasis, Erikssonia, Poecilmitis*,

and *Oxychaeta*, for which sufficient information is available, are obligatorily myrmecophilous. The same is true for most members of *Cigaritis, Axiocerses*, and *Aloeides*. Only in a few species of the latter genera (*Cigaritis allardi, Axiocerses amanga, Aloeides trimeni*) facultative myrmecophily is likely to occur.

In general, the ant hosts belong to the genus *Crematogaster*, but exceptions are documented (*Spindasis vulcanus* and *Axiocerses harpax* also with *Pheidole; Aloeides* and *Erikssonia,* exclusively with *Acantholepis; Axiocerses amanga* and *Poecilmitis pyroeis* with *Camponotus*).

The ant-associations of Aphnaeini are supposedly trophobiotic, the caterpillars providing attractive secretions for their hosts. The larvae of several species are at least sometimes fed with ant regurgitations (surely observed in *Spindasis takanonis* and *Cigaritis acamas,* strongly suspected for *S. nyassae, Axiocerses harpax, A. pseudozeritis*). In some cases, however, available evidence suggests that the larvae may be entirely aphytophagous, possibly feeding on ant brood in nests (*Trimenia, Tylopaedia, Argyrocupha, Oxychaeta*).

Ant-dependent oviposition and specific communication of caterpillars with their host ants (using pheromone mimics from the TOs) are rather well documented in the Aphnaeini. In some species (*Spindasis, Cigaritis, Poecilmitis*) the associations are so close that caterpillars soon die from fungal infections when reared in the absence of their ant hosts, due to the permanent exudation of DNO secretions (Henning 1987, Rojo de la Paz, pers. comm.).

Among the Theclini obligate myrmecophily is less common, but still widespread. Obligatory myrmecophiles are known from four Luciiti genera (*Lucia, Paralucia, Acrodipsas, Hypochrysops*), mostly with the ant genera *Crematogaster* and *Iridomyrmex*. *Acrodipsas* larvae are even predatory on ant brood throughout their larval period (Samson 1989), while the other genera maintain trophobiotic ant-associations.

In the small subtribes Ogyriti (several *Ogyris* species) and Zesiiti (*Zesius, Jalmenus, Pseudalmenus*) obligate myrmecophily is common as well, but only *Zesius chrysomallus* may occasionally feed on ant brood (Yates 1932). Obligate trophobiotic interactions are known from several Arhopaliti (*Arhopala centaurus, A. pseudocentaurus* with *Oecophylla smaragdina*), and three Malaysian *Arhopala* species feed exclusively on myrmecophytic trees of the genus *Macaranga* (Euphorbiaceae) where they are constantly attended by the specific ant partner *Crematogaster borneensis* (Maschwitz et al. 1984). Further Arhopaliti may turn out to be obligate myrmecophiles, even more so because this species-rich subtribe is yet only fragmentarily known.

Within the subtribe Thecliti only one species (*Shirozua jonasi*) is obligatorily associated with the ant *Lasius spathepus*; the caterpillars feed on aphid honeydew and are supposed to receive ant-regurgitations, thus showing a remarkable life-history parallelism to several Miletinae species.

So, obligate myrmecophily occurs in all but one Theclini subtribes with trophobiotic relationships prevailing. Strictly parasitic interactions are confined to one genus

(*Acrodipsas*), while *Zesius* and *Shirozua* are only partly detrimental to their ant-associates.

Compared to the roughly 530 Theclini species worldwide, the number of obligate myrmecophiles is rather low. A conservative estimate yields distinctly less than 200 obligate myrmecophiles (38 %), assuming that some *Hypochrysops*, all *Philiris*, most Thecliti, and at least half of the Arhopaliti are only facultatively myrmecophilous or even secondarily myrmecoxenous. This assumption is in good accordance with the relative figures among the known life-histories in the Theclini, but may well be an overestimate. The proportion of obligate myrmecophiles is certainly significantly higher in the Aphnaeini (>80 %).

In the very large tribe Eumaeini, accounting for one third of the total species diversity of the Lycaenidae, obligate myrmecophiles are almost unknown. Only two closely related *Hypolycaena* species from southern Asia and Australia (*H. erylus, H. phorbas*) are apparently obligatorily associated with *Oecophylla smaragdina* in a trophobiotic way.

From the more than 1000 Eumaeiti species not a single obligate ant-association is hitherto sufficiently documented, nor is any species with ant-parasitic life-habits known. Notwithstanding the scanty knowledge of the larval biology of the Neotropical Eumaeiti, in particular, it is clear that the proportion of obligate myrmecophiles is very low (< 10 %) within the Eumaeini.

In the Polyommatini, obligate myrmecophily is again restricted to a few taxonomic groups. In the Lycaenesthiti, several *Anthene* and *Triclema* species maintain obligate trophobiotic ant-associations, and one (*A. levis*) is even fed by regurgitations of *Crematogaster* ants.

Similarly, the only Niphanditi species whose life-history is known (*Niphanda fusca*) is fed by its specific host ant, *Camponotus japonicus*.

The large subtribe Polyommatiti has two genera with well-documented obligate myrmecophily, the parasitic *Maculinea* and *Lepidochrysops* (see above). Two species of the *Polyommatus* section (*Plebejus argus* and *P. idas*) have recently been shown to maintain quite specific and possibly obligatory trophobiotic ant-associations (e.g. Jutzeler 1989d, e, Ravenscroft 1990), and in some Oriental *Tarucus* species (*T. waterstradti, T. ananda, T. nara*) there is some evidence for obligate myrmecophily as well (Hinton 1951, Maschwitz et al. 1985b).

Assuming that less than one third of the Lycaenesthiti, all Niphanditi, the genera *Maculinea* and *Lepidochrysops*, and a further dozen of Polyommatiti species in other groups are obligatorily myrmecophilous, the proportion of obligate myrmecophiles is well below 200 species (17 %).

Summarizing the current evidence, there is a distinctive systematic disparity with regard to the distribution of obligate myrmecophily in the higher lycaenid taxa. While obligate associations preponderate in the Aphnaeini, and are reasonably common in some Theclini and Miletinae groups, obligate myrmecophily is restricted to very particular taxa in the Polyommatini and is almost entirely unknown from the Eumaeini.

Evidence for obligate ant-associations, often very indirect, is available for only 200 species out of 1000 (20 %) with life-history information available (see Appendix, Tab.17 and 19). Extrapolating on the whole family, most likely less than 800 lyceanid species (< 20 %) are obligatorily associated with specific ants.

It must be emphasized that the estimates presented here are all conservative with respect to the hypotheses of Pierce (1987), i.e. they rather assume too a high proportion of obligate myrmecophily. Obligate ant-associations may well be considerably less numerous in the Theclini and Polyommatini. Nevertheless, single obligatorily myrmecophilous lycaenid taxa are rather species-rich (Aphnaeini, *Lepidochrysops*) and it is plausible to assume that in these taxa the specialization on certain host ants has strongly influenced the evolution, resulting in either a great hostplant range (Pierce & Elgar 1985) or a more rapid speciation (Pierce 1984).

However, as will be discussed in the next chapters, these mechanisms are unlikely to apply for the facultatively myrmecophilous or myrmecoxenous lycaenids, which account for the majority of species (> 75 %).

LYCAENID HOSTPLANT RELATIONSHIPS AND MYRMECOPHILY

Hostplants as selective agents in the Lycaenidae

Myrmecophily of lycaenid caterpillars is mainly mediated by the energetically costly secretions of three types of exocrine epidermal glands (PCOs, DNO, TOs): carbohydrates and amino acids in the DNO secretions (e.g. *Jalmenus, Glaucopsyche, Polyommatus*); possibly amino acids in the PCO secretions (*Glaucopsyche lygdamus* pupae), or ant-brood pheromone mimics in other taxa (e.g. *Lepidochrysops, Maculinea*); and supposedly ant-alarm pheromone mimics from the TOs.

Development and maintenance of the ant-organs (including associated muscles, neurons, cuticular structures etc.) impose additional costs to ant-associated lycaenid caterpillars. The few cost-benefit studies available indeed demonstrated that myrmecophily and its related secretions may result in pupation at a lower final weight associated with reduced fecundity (*Jalmenus evagoras*: Pierce et al. 1987, Elgar & Pierce 1988), or in a prolonged larval period (*Arawacus lincoides*: Robbins in press; see also Henning 1984b).

All energy necessary for both larval development and myrmecophily must be derived from the larval food, viz. usually hostplants. Given these constraints, Pierce (1985) and Pierce & Elgar (1985) have thus argued that the hostplant selection of lycaenids should be strongly influenced by their myrmecophilous life-habits. The idea that hostplant selection could be modified in myrmecophilous species has been presented earlier (e.g. Ehrlich & Raven 1964), and Atsatt (1981b) has shown that *Ogyris amaryllis* females even chose nutritionally inferior hostplants to secure the attendance of specific ants.

Two major hypotheses have been proposed with regard to the possible trade-offs between hostplant selection and lycaenid myrmecophily: the "preference" and the "amplified host range" hypothesis.

The "preference hypothesis"

According to Pierce (1985) myrmecophilous species should tend to utilize energy-rich (and, in particular, protein-rich) hostplants. She proposed that nitrogen-fixing plants from the order Fabales (legumes), parasitic plants from the order Santalales (e.g. mistletoes), or young growth and reproductive plant tissues should be the favourite larval food for ant-associated lycaenids. A widespread predilection of legumes or young growth as larval food in the Lycaenidae has been noted earlier (e.g. Ehrlich & Raven 1964, Cottrell 1984).

Pierce's proposal was substantiated with literature data on the biology of c. 300 species, and recent experiments have confirmed that the quality of larval nutrition may be decisive in maintaining ant-associations. Larvae of *Polyommatus icarus* reared on the legume tree *Robinia pseudoacacia* (a non-host poorly fitting to the nutritive requirements) were far less attractive to ants than those fed herbaceous Fabaceae hostplants (Fiedler 1990c). *Jalmenus evagoras* caterpillars reared on hostplants fertiliz-

ed with additional nitrogen sources became more attractive to ants than those on untreated trees, and the females even preferred such plants for oviposition (Baylis & Pierce 1991).

The "amplified host range hypothesis"

Pierce & Elgar (1985) suggested that myrmecophilous lycaenids should tend to utilize a wider range of hostplants than myrmecoxenous ones, at least in those species where the specific ant-associations are of paramount importance for larval survival. In such species oviposition should largely depend on the presence of appropriate ant partners, and a strong selection for an amplified host range was predicted, with a possible pathway towards speciation (Pierce 1984). Again, literature data were compiled to support this amplified host range hypothesis.

In both studies, however, systematic aspects were neglected, although hostplant relationships among the Lepidoptera are often astonishingly conservative in given systematic groups. While switches in larval hostplants do occur regularly, they in many cases involve either phylogenetically related or chemically similar plant species, suggesting that correlations between hostplant use and phylogeny are common.

Accordingly, attempts have been made to incorporate hostplant relationships in systematic investigations on Lepidoptera (e.g. Downey 1962b), and the concept of coevolution (Ehrlich & Raven 1964) was originally based on the hostplant relationships of butterflies. The theory of coevolution has been the subject of considerable debate ever since, and the unique role of semiochemicals in the formation of plant-herbivore associations has been questioned repeatedly (e.g. Smiley 1985).

Nevertheless, empirical data on hostplant relationships within the Lepidoptera have very often corroborated the existence of phylogenetic patterns. Many subgroups of the largest butterfly family Nymphalidae, for example, are centred on particular taxonomic plant groups (Ackery 1988), or they utilize hostplants that have special semiochemicals in common (Edgar 1984).

The Papilionidae and Pieridae subfamilies and tribes likewise possess characteristic hostplant relationships (e.g. Zerynthiini and Troidini on Aristolochiaceae, Papilionini on Rutaceae and Apiaceae, Dismorphiinae and Coliadinae on Fabales, Pierinae on Capparales), and in these two families secondary plant compounds (glucosinolates, alkaloids etc.) are known to play a leading role in taxon-specific host relations.

Hostplant relationships and food preferences of the Lycaenidae have rarely been used in classificatory attempts, and few authors have tried to cover the whole spectrum of that large family. Ehrlich & Raven (1964) recognized that lycaenids utilize a very broad spectrum of hostplants, approximately equally diverse as that of the more species-rich Nymphalidae. They described only few, rough systematic hostplant patterns (e.g. Lycaenini on Polygonaceae, Thecliti on Fagaceae, Polyommatini on Fabaceae), but this is not amazing given the scanty knowledge of lycaenid life-histories and the lack of a more realistic classification at that time.

The "bewildering array" of lycaenid hostplants largely prevented Ehrlich & Raven and later authors from more detailed analyses, and subsequent studies (Vane-Wright 1978,

Cottrell 1984, Pierce 1985, Ackery 1988) basically adopted Ehrlich's and Raven's view.

With the growing knowledge of lycaenid hostplants, however, several of Ehrlich's and Raven's statements have proven wrong (e.g. lycaenids are now known to utilize ferns, Begoniaceae, Bignoniaceae, Celastraceae, Cucurbitaceae, Myrtaceae, or Rubiaceae as hosts), and today a distinctly broader database concerning lycaenid hostplants is available.

Thus, it seems necessary to reinvestigate in more detail whether or not systematic patterns of hostplant use do occur in the Lycaenidae or in some of their subgroups. If so, these instead of selective pressures arising from myrmecophily might account for a considerable proportion of the extant pattern of hostplant use in that family. Detailed discussions on the hostplants and ant-associations of the Riodinidae were given by Harvey (1987) and DeVries (1990b).

In this chapter I will address the following questions: Do the subfamilies, tribes, subtribes etc. of the Lycaenidae exhibit taxon-specific trends in their hostplant relationships? Do myrmecophilous species really tend to prefer plants of the Fabales or Santalales as suggested by Pierce (1985)? And, do myrmecophilous species really show the amplified hostplant range as predicted by Pierce & Elgar (1985)?

Database and analytical procedure

From more than 200 literature sources I extracted the information concerning larval hostplants (only considered here at family level), ant-associations, and the presence of myrmecophilous organs for more than 1000 lycaenid species. Endophytic feeding habits or preferences for young growth, flowers, or ripening seeds were also noted.

This literature survey was intended to cover the whole systematic spectrum of the Lycaenidae as complete as possible. Since the extensive literature on butterfly hostplants perpetuates a huge number of erroneous records, special attention was paid to include only reliable data into the analysis, although certainly some erroneous records have found their way here again.

The data obtained are of very different quality, ranging from mere oviposition records to detailed ecological studies. To reduce the unevitable bias arising from this, I have considered oviposition records or observations from laboratory rearings only, if closely related species are definitely known to utilize similar plants in nature. Foodplant records from laboratory rearings (a minority) are included because they help demonstrating the physiological potential of the respective species.

Furthermore, the knowledge of lycaenid hostplants is still much less complete than in families like Papilionidae or Nymphalidae, and the distribution of hostplant records is rather uneven among the higher taxa of the Lycaenidae. In total, life-history information was obtained for less than 25 % of the described species, but some species-rich higher taxa (Poritiinae, Arhopaliti, *Jamides* and *Lycaenopsis* section of the Polyommatiti) are distinctly under-represented.

Nevertheless, the database presented in the Appendix is assumed to be sufficiently complete to support the detection of realistic patterns. An increasing knowledge of lycaenid larval biology will certainly modify, but in all probability not reverse these patterns.

To allow quantitative comparisons among the hostplant relationships of the higher Lycaenidae taxa, the hostplant range of the larvae was scored using the number of hostplant families (family index FI; delimitations of plant families following Ehrendorfer 1983) as well as a categorization into the following 5 ranks (range index RI):

1: monophagous (one hostplant species only); 2: stenoligophagous (one hostplant genus); 3: oligophagous (one hostplant familiy); 4: moderately polyphagous (hostplants in two families); 5: polyphagous (hostplants in three or more families).

For all subfamilies, tribes and subtribes the arithmetic means and standard deviations of FI and RI are calculated. These indices facilitate comparisons with the respective figures of Pierce (1985).

In view of the fragmentary knowledge of many lycaenids such a scoring and analysis is necessarily a rough approximation. An analysis using the number and taxonomic relatedness of hostplant species would certainly be more appropriate, but is yet impossible on a worldwide scale.

A detailed survey of the evolution and physiology of hostplant relationships of the Lycaenidae is beyond the scope of this study and requires more complete data. Even for the rather well known Holarctic fauna additions to the hostplant lists are permanently recorded, but new family records are relatively rare.

Thus, the family index FI gives a more reliable, albeit rough estimate of the hostplant spectrum of a butterfly species. A disadvantage of FI is that a few species with exceptional polyphagy (e.g. *Hypochrysops ignitus, Callophrys rubi, Strymon melinus, Celastrina argiolus*) may bias the average FI of a particular taxon. As a consequence, the variance of FI is usually high. This is partly compensated by using the range index RI where the coefficient of variation (the ratio of standard deviation and arithmetic mean) never exceeds 0.54 (up to 1.47 with FI).

On the grounds of this descriptive treatment of lycaenid hostplant relationships I then examine possible trade-offs with myrmecophily. Unfortunately, the presence or absence of preferences for young growth or inflorescences is only sporadically indicated in the literature. Accordingly, this potentially important characteristic had to be excluded from the quantitative analyses. The distribution of host ranges (RI), and the predilection of legumes or mistletoes, are related to the information available on myrmecophily in contingency tables.

Since the records of ant-associations are incomplete in many (especially tropical) taxa, I have tentatively treated such species as myrmecophiles as well, if appropriate information on closely related species is present. These myrmecophily estimates are always conservative, and the strong correlations between phylogeny and ant-associations validate this procedure (see also Fiedler 1991).

A more detailed analysis including the degree of myrmecophily (definitions see Fiedler 1991 and Tab.17 in the Appendix) was omitted in view of the sketchy database.

Quantitative evaluations were normally carried out computing Chi^2 statistics (with Yates' correction). For small "sample sizes" (= species numbers) Fisher's "exact probability" was calculated. Similar analyses were conducted by Pierce (1985) and Pierce & Elgar (1985).

It must, however, be kept in mind that the life-history data only partially fulfill the requirements of a statistical analysis. The Holarctic *Polyommatus* group, for example, is much better known than the equally diverse Oriental subtribe Arhopaliti, exemplifying the distinct Holarctic bias in the recording of lycaenid life-histories. Despite this partial non-randomness of the data, a statistical approach may be helpful in disentangling the complex patterns observed.

The hostplant relationships of the higher lycaenid taxa

Aberrant feeders: Poritiinae and Miletinae

These two subfamilies exhibit striking larval feeding habits largely deviating from the usual herbivory of most lepidopterous caterpillars. The Poritiinae consist of two tribes, one of which, the Oriental Poritiinae, are herbivores of trees (information found only for 1 of c. 50 species).

In contrast, the larvae of the African Liptenini (information found for 58 of the c. 520 spp.) feed on lichen, fungi and similar substrates (throughout this chapter I omit the citations of references to facilitate use; all references used are given in Tab.17 and 19 in the Appendix).

With the possible exception of some Lipteniti whose larvae have always been observed on trees heavily infested with *Crematogaster* ants, Poritiinae caterpillars are strictly myrmecoxenous. Since these presumed myrmecophiles feed on the same substrates as their myrmecoxenous counterparts, no evidence for effects of myrmecophily on larval nutrition can be found among the Liptenini. As the taxonomic host ranges of most of the lichen feeders are unknown, a discussion of the host range hypothesis must be deferred.

The specialization on lichen or fungi, however, may be an important prerequisite for one evolutionary route leading to myrmecophily: caterpillars able to feed on such substrates are physiologically adapted to metabolize chitin (which is an important compound of fungi; cf. Rawling 1984) and may start to utilize fungi or even remains of ants in ant nests. The lichen-feeding arctiid moth *Crambidia casta* could represent a parallel case for this evolutionary route towards myrmecophily (Ayre 1958).

Miletinae larvae (information found on 37 of c. 140 spp.) are entirely aphytophagous, feeding on Homoptera, ant brood, honeydew, or ant regurgitations. Only part of the Miletinae caterpillars are undoubtedly myrmecophilous, but these utilize basically similar and equally protein-rich food-substrates as their myrmecoxenous relatives.

Consequently, no trade-offs between larval food and degree of myrmecophily can be observed. Some Miletinae species (e.g. *Allotinus unicolor, Miletus* spp.) are specifically

associated with certain ants and are presumed to feed on a rather broad variety of Homoptera (Maschwitz et al. 1988, Fiedler & Maschwitz 1989c). However, since most obligatorily myrmecophilous Miletinae are predators or parasites of their specific host ants only, this evidence supporting the host range hypothesis is very limited. The carnivorous feeding habits of Miletinae immatures provide a set of preadaptations for another independent pathway leading to myrmecophily (Cottrell 1984, this study).

The remaining lycaenid subfamilies are primarily herbivorous, and a meaningful discussion of the hypotheses of Pierce (1985) and Pierce & Elgar (1985) has to be restricted to them.

Curetinae

This small group feeds almost exclusively on legumes (information found for 6 of the 18 spp.; RI = 3.17 ± 0.41 , FI = 1.17 ± 0.41) with strong preference for young growth (DeVries 1984, Maschwitz & Fiedler, unpublished). These are exactly the conditions where myrmecophily should be expected according to Pierce (1985). However, *Curetis* larvae are not truly myrmecophilous, as has been explained in detail above.

Lycaeninae

This large subfamily contains more than 3,640 species, i.e. more than 80 % of the whole species diversity of the family Lycaenidae. Because of this and the large heterogeneity of several groups with regard to their feeding preferences and myrmecophilous relationships, the tribes and subtribes will be treated separately.

Aphnaeini — Larvae of this mainly African tribe (information present for 77 of about 250 spp.) utilize a broad range of at least 32 hostplant families. Thirty-eight species feed on legumes (at least in captivity), other well-represented plant families are Zygophyllaceae (16 species) and Asteraceae (13 species; both mainly in the genus *Poecilmitis*). Plants of the order Santalales are mentioned as larval food for only five species.

Several members of the Aphnaeini are known or at least strongly suspected to be aphytophagous; five species of the genera *Spindasis, Cigaritis* and *Axiocerses* are fed by *Crematogaster* ants with regurgitations, *Oxychaeta dicksoni* seemingly feeds on *Crematogaster* brood, and the genera *Tylopaedia, Trimenia* and *Argyrocupha* are suspected to be entirely aphytophagous.

Aphnaeini larvae exhibit an extraordinarily high degree of myrmecophily. No single species is known to be myrmecoxenous, but as many as 80 % of the species where information is present are strongly or even obligatorily associated with ants.

Although the Aphnaeini are among the most strongly myrmecophilous lycaenids, and nutritive liquids are secreted by the larvae of some species in high amounts, a correlation between larval hostplants and ant-associations is not apparent. For example, legumes are only weakly represented in the hostplant list of the obligately myrmecophilous genus *Poecilmitis* and are not used by *Phasis* at all.

About half of the myrmecophilous Aphnaeini species are not associated with legumes. However, the taxonomically widespread use of Fabales as hosts indicates that these may be the primary hostplant group of the tribe. The statistical evaluation shows (Tab.5) that obligatorily and facultatively myrmecophilous Aphnaeini species do not differ in their use of legumes as hosts. A preference for young growth or flowers has been reported for only 10 species suggesting that this trend is not well developed in the Aphnaeini. So, the predilection hypothesis does not apply to this tribe, nor does the host range hypothesis.

Most Aphnaeini species are confined to one foodplant family, while only 20 (including 7 laboratory records) have been reported to utilize at least two plant families (RI = 2.72 ± 1.20; FI = 1.53 ± 1.09; n = 71 herbivorous species). The host ranges of obligatory and facultative myrmecophiles among the Aphnaeini cannot be distinguished statistically (Tab.5).

Rather, there appears to exist a systematic pattern: polyphagous species within the Aphnaeini mainly occur in the genera *Spindasis* and *Poecilmitis*, whereas species of *Cigaritis, Axiocerses, Phasis* and *Aloeides* tend to be oligophagous, suggesting that the former two have a better developed potential for polyphagy, whereas the latter four are basically food specialists. The high degree of myrmecophily, however, does not differ between these taxa.

Tab.5: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Aphnaeini (obl: obligate myrmecophiles, fac: facultative myrmecophiles). Given are absolute species numbers (database see Appendix). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
obl	48	16	> 0.8
fac	5	3	

hostplants	Fabales	other plants	P
obl	32	31	> 0.8
fac	5	3	

Lycaenini — This small tribe of nearly worldwide distribution has very homogeneous hostplant relationships. The larvae feed primarily on Polygonaceae (information found for 38 of c. 95 spp.) with exceptions known from only six Nearctic species (on Rosaceae, Ericaceae, Rhamnaceae, Grossulariaceae). Doubtful records include Fabaceae (*Lycaena thersamon*) and Chenopodiaceae (*L. phoebus*, oviposition record only). At least for one group of closely related species (*Lycaena helloides/dorcas*), the hostplant shift from Polygonaceae to Rosaceae is correlated with similar allelochemicals in the plant species involved (Ferris 1979).

The hostplant range of all species is narrow, normally covering only one plant genus (RI = 2.08 ± 0.59, FI = 1.03 ± 0.16, n = 38). European Lycaeninae larvae are usually

myrmecoxenous and ant-associations have only exceptionally been observed (*Lycaena dispar*: Cottrell 1984). Other *Lycaena* caterpillars (*L. virgaureae, ottomanus, alciphron, hippothoe, phlaeas, tityrus*) sometimes induce ant-associations in the laboratory (Malicky 1969, this study), but this has not been confirmed in the field.

Only four Nearctic species are regularly attended by ants (*L. heteronea, L. rubidus, L. xanthoides, L. editha*: Ballmer & Pratt 1988). All these species feed exclusively on foliage of Polygonaceae, and there is no indication of any trade-offs between hostplant use and the low level of myrmecophily in a couple of species among the Lycaenini. Neither the predilection nor the host range hypothesis receives support from the hostplant relationships of this tribe.

Theclini

Luciiti

The Theclini comprise about 530 species in 5 subtribes with biological information available for 120 species. The Australian Luciiti (c. 150 spp., information found for 43) utilize a remarkably large spectrum of at least 36 hostplant families, including ferns (*Hypochrysops theon*), monocots (Dioscoreaceae: *Pseudodipsas, Hypochrysops*), and Lauraceae (*Philiris* spp.). Legumes and parasitic plants of the order Santalales are only weakly represented as hosts (four species each).

A general hostplant pattern of the Luciiti is not yet apparent, but several genera show specific feeding habits: *Paralucia* on Pittosporaceae, *Philiris* on Lauraceae, Urticales and Euphorbiaceae. *Acrodipsas* larvae are predators of *Crematogaster* and *Iridomyrmex* brood. *Pseudodipsas* and *Hypochrysops* are polyphagous genera, *H. ignitus* alone being recorded from 17 plant families.

The caterpillars of all genera but *Philiris* are usually myrmecophilous, several species in the genera *Lucia, Paralucia, Pseudodipsas, Acrodipsas* and *Hypochrysops* even obligatorily so. However, as already mentioned by Valentine & Johnson (1989), there is no indication of a preference for protein-rich hostplant families in the myrmecophilous Luciiti, and this view is corroborated by the statistical evaluation of the life-history information (Tab.6).

Actually all Luciiti species feeding on legumes or mistletoes are myrmecophilous, while no myrmecoxenous species are known to feed on these plants. But this result is only marginally statistically significant for legumes plus mistletoes (Fisher's $P = 0.058$), and not at all significant for legumes alone. A predilection of young growth is only recorded from three genera (*Paralucia, Pseudodipsas, Hypochrysops*).

The host range hypothesis receives more support in the Luciiti. On average, Luciiti larvae are moderately polyphagous ($RI = 2.41 \pm 1.31$; $FI = 2.16 \pm 3.18$; $n = 38$ phytophagous spp.). Host ranges of obligatory and facultative myrmecophiles are similar, but polyphagous species exclusively occur among the myrmecophiles, whereas the myrmecoxenous members of *Philiris* are apparently all confined to one hostplant familiy or even genus (Tab.6; see also Valentine & Johnson 1988, 1989).

Nevertheless, this host range difference is again just marginally significant, and polyphagy is recorded from only seven species of *Pseudodipsas* and *Hypochrysops*, while 21 myrmecophilous Luciiti species have thus far been reported from one single hostplant family. So, it is well possible that the amplified hostplant ranges of *Pseudodipsas* and *Hypochrysops* indicate a phyletic predisposition for, rather than a consequence of, ant-dependent foodplant choice.

Tab.6: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid subtribe Luciiti (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
obl	11	4	> 0.8
fac	9	3	
phil	20	7	0.058
xen	12	0	

hostplants	Fabales	other plants	P
obl	3	12	0.61
fac	1	11	
phil	4	23	0.21
xen	0	12	

Ogyriti

This small Australian tribe contains only 15 species, the life-histories of 12 being known. All utilize Loranthaceae or the closely related Santalaceae as hostplants, thus showing a remarkably homogeneous hostplant range (RI = 2.50 ± 0.52; FI = 1.00 ± 0.00; n = 12). This strongly suggests a taxon-characteristic and evolutionarily stable adaptation towards similar allelochemicals of the Santalales.

Probably all Ogyriti larvae are ant-associated and possess a full complement of ant-organs, with some species (e.g. *Ogyris genoveva, O. otanes, O. amaryllis*) probably being obligatorily myrmecophilous. At least one species, *O. amaryllis*, uses ants as oviposition cues (Atsatt 1981b). The confinement of Ogyriti to Santalales as hostplants agrees well with the preference hypothesis of Pierce (1985), but gives no support to the amplified host range hypothesis.

Zesiiti

This subtribe comprises 11 species in southern Asia and Australia with life-history information available for all of them. Zesiiti larvae feed on legumes, but four species utilize additional families (*Zesius*: Combretaceae, Dioscoreaceae; *Jalmenus*: Sapindaceae, Myrtaceae). The hostplant range (RI = 2.82 ± 1.47; FI = 1.73 ± 1.01; n = 11) is moderate.

All Zesiiti are myrmecophilous, at least half of them even obligatorily so. The ant-associated Zesiiti show the preference for nitrogen-fixing plants and young plant tissue postulated by Pierce (1985), and the experimental work of Baylis & Pierce (1991) clearly demonstrates the importance of the nutritive quality of larval food for maintaining ant-associations.

However, the Zesiiti hostplant pattern does not consistently support the amplified host range hypothesis. While some of the obligatorily myrmecophilous species utilize several plant families (*Zesius chrysomallus, Jalmenus ictinus, J. pseudictinus*), others are clearly confined to a single plant genus (*J. evagoras, Pseudalmenus chlorinda* on *Acacia*). In all, the Zesiiti hostplant pattern is indicative of a primary association with young growth of legumes and some secondary amplifications towards Sapindaceae, Combretaceae or Myrtaceae.

Interestingly the same plant families are utilized by several other lycaenids feeding primarily on Fabales (*Hypolycaena, Deudorix, Anthene*) and also by the nymphalid tribe Charaxini (Ackery 1988), suggesting that the chemical barriers opposing these particular hostplant shifts are low.

Arhopaliti

This large tribe contains about 240 species with peak diversity in South East Asia. Information on larval biology (20 spp. only) is very scanty. Hostplant families include Fagaceae and Euphorbiaceae (both for six species), Myrtaceae, Lythraceae and Combretaceae (each for four species), totalling 13 families. Legumes and mistletoes are mentioned for only one species each.

Facing this fragmentary knowledge, the only tentative statement yet possible is that Arhopaliti larvae feed upon a wide range ($RI = 3.06 \pm 1.66$; $FI = 2.00 \pm 1.66$; $n = 16$) of broad-leaved trees, apparently preferring young growth, but neither predilecting Fabales nor Santalales.

Myrmecophily seems to be the rule in the Arhopaliti, and some members are obligatorily associated with a single ant species (e.g. *Arhopala centaurus, A. pseudocentaurus* with *Oecophylla smaragdina*). These two *Arhopala* species are highly polyphagous and may provide examples for the amplified hostplant range in response to obligate and specific ant-associations. Three other *Arhopala* species, in contrast, are monophagous on myrmecophytic *Macaranga* trees (Euphorbiaceae) where they live in close association with the appropriate symbiotic ant of these trees, *Crematogaster borneensis*. Hence, specific ant-associations in the genus *Arhopala* are not necessarily correlated with a wide hostplant range.

The current poor knowledge of Arhopaliti biology precludes any conclusive discussion of this subject, while the preference hypothesis is not at all supported by the data available.

Thecliti

The larval biology of this predominantly Asiatic subtribe is considerably better known (information found for 34 of c. 120 species). As was already pointed out by Shirôzu

(1962), the primary Thecliti hostplant family are the Fagaceae, reported as hosts for 22 species (including laboratory records).

Additional related plant families of the Hamamelididae (Hamamelidaceae, Betulaceae, Corylaceae, Myricaceae, Juglandaceae, Ulmaceae) are utilized by some species. One group of related genera feeds on Oleaceae. Rather exceptional are the associations with Rosaceae (*Thecla, Chrysozephyrus smaragdinus*) or Ericaceae (*Chrysozephyrus birupa*). *Shirozua jonasi* feeds on aphids and regurgitations of the ant *Lasius spathepus*, and the taxonomically isolated *Amblopala avidiena* is the only Thecliti species reported from legumes.

Hence, although 12 plant families are involved, the hostplant associations of the Thecliti show a distinct pattern: a predilection of Hamamelididae trees (mainly Fagaceae) which typically contain high amounts of tannins and often possess ethereal oils. Interestingly the unrelated Eumaeiti genus *Satyrium* s. l. shows a parallel hostplant pattern with 11 species on Hamamelididae, 10 on Rosaceae, and two on Ericaceae and Oleacae, suggesting that chemical similarities have independently governed the evolution of hostplant use in these two taxa of temperate woodlands.

The hostplant range of most Thecliti species is rather narrow (RI $= 2.56 \pm 1.05$; FI $= 1.32 \pm 0.84$; n $= 34$), and at least some species preferentially or exclusively feed on young growth or reproductive tissues of their hosts. Several of the records cited by Shirôzu (e.g. for *Thecla betulae* and *Quercusia quercus*) are only rare occasional hostplants or result from laboratory findings, because these two Palaearctic species are usually known from Europe to utilize only one plant family in nature (Rosaceae and Fagaceae, respectively).

Most Thecliti larvae lack the typical ant-organs, and records of ant-associations are rare among this subtribe except for some old reports of ant-associations of *Thecla betulae* (Malicky 1969; possibly derived from artificial trials: Emmet & Heath 1990). However, ants attend pupae of *Thecla betulae* and *Quercusia quercus* (Emmet & Heath 1990), and *Shirozua jonasi* is obligatorily myrmecophilous. Anyway, since most Thecliti exhibit only a low degree of myrmecophily, a discussion of the preference or host range hypothesis within this subtribe would be misplaced. *Amblopala avidiena* appears to be the only known Thecliti species possessing a DNO and TOs. This morphological trait and the hostplant relationship with legumes challenge its current systematic position.

Thecliti and Arhopaliti are presumed to be sister-groups (Eliot 1973). Interestingly, Fagaceae are well represented among their hostplants and both show no preference for legumes. This common hostplant pattern supports the idea that Thecliti may be derived from Arhopaliti-like ancestors. The subsequent reduction of myrmecophily among the Thecliti might then be attributed to the rather poor nutritive quality of Fagaceae trees in concert with the relative paucity of ants foraging in the canopy of temperate zone woodlands.

The hostplant pattern of Theclini as a whole is rather obscure, and this again emphasizes the heterogeneity of this taxon of questionable monophyly. Fifty hostplant families are utilized by 111 species for which adequate information is available. Twenty-

eight species feed on Fagaceae, 17 on legumes, 15 on Loranthaceae, 11 on Euphorbiaceae, 10 on Myrtaceae, 8 on Sapindaceae and Combretaceae, 7 on Oleaceae, 6 on Lauraceae and Verbenaceae, and 5 on Rosaceae. Twenty hostplant families are hitherto recorded for only one single Theclini species. This is indicative of an overall high diversity of larval hosts (mainly broad-leaved trees and shrubs or epiphytes, rarely non-woody plants), in particular among the most diverse subtribes Luciiti and Arhopaliti. The majority of Theclini larvae are oligophagous (RI = 2.60 ± 1.23, FI = 1.68 ± 2.06, n = 111). Only 22 species are recorded from two or more hostplant families (Tab.7), but polyphagy is significantly more common among the myrmecophiles. However, there is no difference in the host range between obligate and facultative myrmecophiles, as would be expected if ant-dependent hostplant selection were the primary selective force towards polyphagy.

A predilection of Fabales or Santalales only exists in small subgroups (Ogyriti, Zesiiti). All species feeding on these plants are myrmecophilous, while myrmecoxenous Theclini consistently use other plant families as larval hosts. This results in a statistically significant difference between the hostplant associations of myrmecophilous and myrmecoxenous Theclini (Tab.7), but with respect to the scant information and the systematic trends outlined above generalizations should be taken with caution.

Although the preference hypothesis of Pierce (1985) receives some support when viewing on the whole tribe Theclini, more than half of its myrmecophilous members are not known to feed on Fabales or Santalales. Remarkably, there is no Theclini subtribe to which both the preference and host range hypothesis consistently apply. Myrmecophilous Ogyriti and Zesiiti predilect Fabales and Santalales, but are mostly oligophagous. In contrast, the myrmecophilous Luciiti and Arhopaliti, albeit rather polyphagous, do not utilize the postulated plant taxa to a greater extent.

Eumaeini

The Eumaeini are by far the largest lycaenid tribe with c. 1.580 described species. The monophyly of this grouping (sensu Scott & Wright 1990) is not sufficiently confirmed, and its subdivision is far from being satisfactory. In addition, the predominantly Neotropical Eumaeiti (the largest subtribe with over 1.000 species) are poorly known with regard to their taxonomy and larval biology. Thus, the following discussion of Eumaeini hostplant patterns and myrmecophily is necessarily tentative.

Catapaecilmatiti

This small Oriental tribe comprises only 11 species in two genera. Information is only available for *Catapaecilma* whose highly myrmecophilous larvae feed on young shoots of Combretaceae, thus neither confirming the preference nor the host-range hypothesis.

Amblypodiiti

A small Palaeotropical group (c. 13 species, information available on 8), feeding on young growth of Olacaceae (*Amblypodia*) or Moraceae (*Iraota, Myrina*). The larvae possess a DNO and TOs and are usually myrmecophilous. The ant-associations

Tab.7: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Theclini (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). P: probability of Chi^2 statistics for 2x2 contingency tables.

RI	1—3	4/5	P
obl	21	9	0.755
fac	29	9	
phil	50	18	0.047
xen	39	4	

hostplants	Fabales	other plants	P
obl	9	21	0.58
fac	8	30	
phil	17	51	0.001
xen	0	43	

hostplants	Fabales + Santalales	other plants	P
obl	13	17	0.592
fac	19	19	
phil	32	36	< 0.001
xen	0	43	

reported are facultative and rather loose (*Amblypodia anita* is stated to have no ant-associations despite its ant-organs: Bell 1915). All species are oligophagous and do neither feed on legumes nor on mistletoes, but show a preference for young plant tissue.

Loxuriti

The Loxuriti contain nearly 60 species (information available for 11 species) and are subdivided in three groups (treated as subtribes in Scott & Wright 1990). Two of these have characteristic hostplant preferences, the *Loxura* group feeding on young growth of monocots (Dioscoreaceae, Smilacaceae), whereas the *Cheritra* group mainly utilizes young growth of Fabales (but also Rubiaceae, Myrtaceae and Lauraceae). The *Horaga* group has hostplant records from Euphorbiaceae, Coriariaceae, Myrtaceae, Styracaceae, Rubiaceae, and Sapindaceae. As a whole, Loxuriti utilize 12 hostplant families and are rather polyphagous (RI = 3.18 ± 1.40, FI = 2.18 ± 1.47, n = 11).

Loxuriti larvae are usually myrmecophilous, although information regarding myrmecophily in *Horaga* and *Rathinda* is missing. *Cheritra freija* is polyphagous on young growth including legumes, but is myrmecoxenous in contrast to the predicitions of the preference and host range hypothesis. Species of the *Loxura* group are oligophagous, but ant-associated. Hence, the limited information available for this sub-

tribe does not support any of both hypotheses, but indicates that taxon-characteristic hostplant relationships and a basic preference for young plant growth are prevalent.

Iolaiti

The hostplant relationships within this subtribe are astonishingly monotonous (RI = 2.22 ± 0.73, FI = 1.06 ± 0.24). All 64 species for which information is available live on Loranthaceae or on the closely related Olacaceae (6 species). Single deviating records (e.g. Verbenaceae for *Tajuria diaeus*) most likely refer to the host trees on which the true hostplants (mistletoes) grow.

However, ant-associations are seemingly not very strongly developed, and sure records exist for only eight species. Several of these are stated to be just very occasionally attended by ants (e.g. Bell 1915). In a number of species the presence of larval ant-organs has been denied, albeit the records are partially controversial. Though more ant-associations will almost certainly be detected if the arboricolous Iolaiti larvae will receive a closer study in the field (especially the species where ant-organs are undoubtedly present), the morphological and behavioural observations strongly suggest that myrmecophily is rather weakly developed among the Iolaiti.

This sharply contrasts to the preference hypothesis (mistletoe-feeders are expected to show a high degree of myrmecophily), and the host range hypothesis does not apply to this oligophagous subtribe at all.

Remelaniti

Nothing is known concerning the larval biology of this small group (seven species) except hostplant records for two species (Loranthaceae, Ericaceae, Hypericaceae, Myrsinaceae), and any discussion must await further information.

Hypolycaeniti

This Afro-Oriental subtribe consists of two genera (sensu lato) with characteristic larval nutrition (information available for 11 of c. 55 species). The African genus *Leptomyrina* feeds inside the leaves of succulent plants in arid regions (mainly Crassulaceae, also Aizoaceae). *Hypolycaena* caterpillars are basically polyphagous with a distinct predilection of young foliage and inflorescences, but three species are specialists solely feeding upon Orchidaceae flowers.

As a whole, Hypolycaeniti larvae are polyphagous (RI = 3.73 ± 0.79, FI = 2.81 ± 3.12, n = 11) and utilize 19 hostplant families with no predilection of legumes or mistletoes.

All species are supposedly myrmecophilous irrespective of their host ranges or preferences. Two Oriental species (*Hypolycaena phorbas, H. erylus*) are probably obligate myrmecophiles with a very wide host range and could thus be seen as examples of amplified host ranges in response to specific myrmecophily. However, another African species (*H. philippus*) is likewise extremely polyphagous (at least eight

hostplant families), but is unspecifically associated with ants from two subfamilies. So, neither the host range nor the preference hypothesis are generally valid for the larvae of Hypolycaeniti.

Deudorigiti

The larvae of this largely Afro-Oriental subtribe (information available for 46 out of c. 200 species) utilize at least 31 plant families as hosts with a distinctive preference for legumes (recorded for 26 species). Other important hostplants belong to the Sapindaceae, Rosaceae and Myrtaceae (8 species each), Proteaceae (7 species), and Rubiaceae (6 species). Mistletoes play almost no role as larval hosts. Practically all Deudorigiti larvae preferentially or exclusively feed on particularly nutritive plant tissues like young foliage, flowers or ripening seeds.

Facultative myrmecophily is widespread among the Deudorigiti, but reductions occur in some groups with larvae feeding inside flowers or fruits (*Bindahara, Capys*, some *Deudorix* species). There is a significant relationship between hostplant preference and myrmecophily (Tab.8): reductions of myrmecophily are unknown from species feeding on legumes.

As a whole, Deudorigiti larvae are rather polyphagous (RI = 2.82 ± 1.51, FI = 2.57 ± 2.72, n = 44), although the majority of species is known from only one hostplant family. However, myrmecoxeny is known exclusively among food specialists, whereas truly polyphagous species are generally associated with ants, resulting in a significant relationship between polyphagy and myrmecophily. Hence, both the preference and the host range hypothesis are supported by evidence from the subtribe Deudorigiti.

Eumaeiti

Biological information on this most diverse of all lycaenid subtribes is still rather scanty and only allows a tentative discussion. In the following analysis 221 species are considered including a bulk of unpublished data on Neotropical species kindly communicated by Robbins (these are not given in the Appendix).

Eumaeiti hostplant records cover no less than 90 plant families. With 56 entries legumes are mentioned most often, followed by Rosaceae (20 species), Fagaceae (17), Solanaceae (13), Sapindaceae, Euphorbiaceae, Loranthaceae, Asteraceae (12), Polygonaceae (11), and Rhamnaceae and Verbenaceae (10). Unusual lycaenid hostplants are cycads (5 species), conifers (11), or monocots (14). Families not known to serve as lycaenid hosts outside the Eumaeiti are Cactaceae, Apocynaceae and Asclepiadaceae. The larvae of at least one species are even predators of Homoptera (Boulard 1986).

In all, the available data are indicative of a highly diverse pattern of hostplant use, although several genera or species groups exhibit taxon-specific hostplant preferences (e.g. *Eumaeus* on cycads, *Allosmaitia* on Malpighiaceae, *Atlides* on Loranthaceae, *Arawacus* on Solanaceae). Legumes are recorded for only one quarter of the Eumaeiti species documented. Most Eumaeiti larvae typically feed on young growth, inflorescences or fruits, many of them even have endophytic life-habits.

Tab.8: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid subtribe Deudorigiti (phil: myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (only 33 species are considered where a reasonable assignment regarding larval ant-associations is yet possible [see Appendix]; a separate analysis based on tentative assignments for some *Deudorix* species [total n = 45] yielded identical statistical results). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
phil	14	12	0.027
xen	7	0	

hostplants	Fabales	other plants	P
phil	22	4	< 0.001
xen	0	7	

Since data on ant-associations of Eumaeiti immatures are exceedingly fragmentary, only some features shall be mentioned here. A thorough analysis must be deferred. Only four of the recorded 26 myrmecophilous species, and only 13 of the supposed 51 myrmecophiles (a low conservative estimate) feed on legumes, the respective figures for mistletoes being one and five species (these figures only concern the species with information available). Thus, the preference hypothesis appears to be invalid for Eumaeiti larvae.

On average, the host range of Eumaeiti caterpillars is moderate (RI = 2.63 ± 1.39, FI = 1.97 ± 2.86, n = 211). However, a number of species is highly polyphagous, *Strymon melinus* being recorded from more than 30 plant families (possibly the most polyphagous butterfly species in the world). Twenty-six polyphagous species with RI = 5 (i.e. with three or more hostplant families) have not yet been recorded to be attended by ants, whereas only 8 of 26 known myrmecophiles (and 11 of 51 presumed myrmecophiles) utilize two or more hostplant families.

Hence, there is no evidence for amplified host ranges among ant-associated Eumaeiti larvae. Rather, highly polyphagous Eumaeiti species (that are all specialized flower- or fruit-feeders) tend to be weakly myrmecophilous or myrmecoxenous.

The patterns of hostplant use and myrmecophily of the two sister-groups Deudorigiti and Eumaeiti differ remarkably. The widespread use of legumes and inflorescences as larval food in both subtribes suggests that the presumably myrmecophilous larvae of their common ancestor also fed on such plant parts. Deudorigiti larvae mostly retained myrmecophily as well as the predilection of legumes and nutritive plant parts. Eumaeiti larvae still predilect protein-rich plant tissues, but their preference for legumes is low, the range of utilized hostplant taxa has been enormously amplified, and polyphagy is often correlated with reductions of myrmecophily.

An overall discussion of Eumaeini hostplant relationships and its possible trade-offs with myrmecophily is yet impossible given the meagre database for Neotropical Eumaeiti. Even an analysis restricted to the Old World subtribes must remain un-

satisfactory since information on ant-associations of Iolaiti and Deudorigiti is very incomplete.

A tentative calculation based on 90 Old World species, for which a reasonable assignment of the degree of myrmecophily is currently possible (i.e. omitting several African *Iolaus* and *Deudorix* species), yields significant relationships between myrmecophily and the preference for legumes ($Chi^2 = 6.31$), or between ant-association and host range ($Chi^2 = 4.01$, $p < 0.05$ for both). Given the taxonomic heterogeneity of the subtribes considered, and in view of the questionable monophyly of the Eumaeini as a whole, these statistical results must be viewed with great caution.

Polyommatini

Candaliditi

This Austro-Melanesian subtribe has a very heterogeneous hostplant pattern (RI = 3.38 ± 1.39, FI = 2.23 ± 1.63, n = 13). Eighteen families have been recorded. A general preference is not apparent. Five species utilize Lauraceae, while only two feed on legumes.

Ant-associations are known or suspected from the majority of species, irrespective of the hostplant taxa and the width of the host range. One species stated to lack ant-associations (*Adaluma urumelia*) feeds on Rutaceae. There is no evidence that the hostplant use of Candaliditi larvae follows the predictions of the preference or host range hypothesis.

Lycaenesthiti

Lycaenesthiti caterpillars have been recorded from 20 hostplant families and are on average rather polyphagous (RI = 3.12 ± 1.30, FI = 2.29 ± 2.16, n = 24). They exhibit a pronounced preference for legumes (16 species) as well as for young growth and inflorescences. Some of the obligate myrmecophiles have an amplified host range (e.g. *Anthene emolus*: Fiedler & Maschwitz 1989b), while others are food specialists. In all, the hostplant relationships of Lycaenesthiti clearly support both the preference and host range hypothesis.

Niphanditi

The only species with well-documented life-history feeds on Fagaceae and is obligatorily myrmecophilous, but this isolated information precludes further interpretations.

Polyommatiti

The larvae of this large subtribe utilize hostplants in at least 70 families. Nevertheless, distinct patterns are apparent. Legumes are highly preferred (157 species), followed by Lamiaceae (34), Rhamnaceae (24), Geraniaceae (17), Sapindaceae (15), Polygonaceae and Selaginaceae (14), and Rosaceae (12). Mistletoes are rarely used as hosts (two species).

On the genus or species group level, further very characteristic hostplant relationships can be observed (e.g. *Lepidochrysops* and *Pseudophilotes* on Lamiaceae, subgenera *Aricia* and *Agriades* of *Polyommatus* on Geraniaceae and Primulaceae respectively, the *Castalius* section on Rhamnaceae), but a more detailed analysis is beyond the scope of the present study. On average, most Polyommatiti larvae are oligophagous (RI = 2.57 ± 1.14, FI = 1.46 ± 1.47, n = 311).

A statistical analysis of the relationships between myrmecophily and hostplant use in the whole tribe Polyommatini yields interesting results. Myrmecoxenous Polyommatini significantly less often feed on legumes than their myrmecophilous relatives.

However, when comparing obligate and facultative myrmecophiles, the reverse result is highly significant: only very few obligatorily ant-associated Polyommatini use legumes as larval hosts (Tab.9). Furthermore, nearly half of the ant-associated species do not feed on legumes. Thus, it is questionable whether the predilection of legumes among Polyommatini larvae is really connected with myrmecophily (see below).

With regard to the host range, no significant differences between facultative and obligatory myrmecophiles, or between myrmecophilous and myrmecoxenous species can be found. In all these categories among the Polyommatini, less than 25 % of the species are truly polyphagous. So, even obligatorily ant-associated species, where ant-dependent oviposition is expected to occur, are mostly restricted to a single hostplant family or even genus.

Conclusions

General patterns of hostplant use within the Lycaenidae

As all other species-rich Lepidoptera families, the Lycaenidae utilize a diverse hostplant spectrum with records available from at least 144 plant families (Tab.18 in the Appendix; Ehrlich & Raven [1964] mention only 85 families for Lycaenidae and Riodinidae together).

However, 77 families have yet been recorded as hosts for three or less lycaenid species and are thus considered to be exceptional host taxa, either used only by a few food specialists, or serving as occasional hosts of polyphagous caterpillars. 35 families are utilized by 10 or more species and can hence be considered to constitute the main hostplant taxa of the Lycaenidae.

The taxonomically widespread connection with legumes (especially Curetinae, Aphnaeini, Zesiiti, Deudorigiti, Polyommatini) supports the assumption that Fabales were the hostplants of ancestral Lycaenidae. However, this hypothesis needs a careful inspection, based on a thorough outgroup comparison and a more complete knowledge of Poritiini hostplants.

Available hostplant data on the oldest lineages of the Nymphalidae (Libytheinae: Ulmaceae) and Riodinidae (Hamearinae: Myrsinaceae and Primulaceae; Harvey 1987) do neither support nor contradict an ancestral Lycaenidae-Fabales connection.

Tab.9: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Polyommatini (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). P: probability of Chi² statistics for 2x2 contingency tables.

RI	1—3	4/5	P
obl	43	11	0.67
fac	200	60	
phil	243	71	0.68
xen	31	5	

hostplants	Fabales	other plants	P
obl	7	47	0.001
fac	161	99	
phil	168	146	0.001
xen	8	28	

Scott (1985) has even suggested that legumes were the ancestral hosts of the Papilionoidea as a whole, and this view is substantiated by the widespred use of Fabales as hosts in those subfamilies of most butterfly families retaining a number of plesiomorphic character states (Hesperiidae-Pyrginae, Papilionidae-Baroniinae, Pieridae-Dismorphiinae and Coliadinae: Scott & Wright 1990).

Again, however, an outgroup comparison yields no decision: the larvae of Hedylidae, the sister-family of the butterflies, are hitherto reported from Sterculiaceae, Malvaceae, and Euphorbiaceae (Scoble 1990).

Legumes by far lead the list of lycaenid hostplant records with entries for 322 species (questionable records omitted), but notably these are less than one third of the lycaenid species for which life-history information is available. Thus, even if nitrogen-fixing legumes are the most widespread, and presumably the ancestral, hostplants of caterpillars of the family Lycaenidae, they probably serve as hosts for less than 40 % of the extant species.

Other plant families of the subclass Rosidae that are well represented in the lycaenid hostplant list include: Loranthaceae (100), Sapindaceae (55), Rosaceae (49), Rhamnaceae (43), Euphorbiaceae (37), Myrtaceae (29), Combretaceae (27), Zygophyllaceae (21), Anacardiaceae and Crassulaceae (19), Geraniaceae (18), Proteaceae (15), and Malpighiaceae (12).

In all, plants out of at least 47 Rosidae families are utilized as hosts by larvae of 652 lycaenid species, and this subclass is hence by far the predominant hostplant group. However, the Aralianae families with their characteristic resins or ethereal oils are only very weakly represented.

The second important angiosperm subclass containing the hostplants of at least 137 lycaenid species are the Lamiidae. Important families are Lamiaceae (37) and the closely

related Selaginaceae (14), Verbenaceae (29), and Bignoniaceae (11) in the Scrophularianae, Solanaceae (15) and Boraginaceae (13) in the Solananae, and Rubiaceae (18) and Oleaceae (12) in the Gentiananae, whereas most Gentiananae families with their characteristic toxic alkaloids, such as Apocynaceae, Asclepiadaceae, or Loganiaceae, only exceptionally serve as hosts for lycaenid caterpillars.

Plant species of the Hamamelididae (here treated after Ehrendorfer 1983, i.e. including the Urticales often transferred to the Dilleniidae) are fed upon by 74 lycaenids (Fagaceae [48 species], Moraceae [12], Ulmaceae [10], and eight further families). Among the Caryophyllidae families only the Polygonaceae are utilized by a larger number of lycaenids (58 species), while nine further families together house only 17 species. Remarkably, Polygonaceae lack the typical caryophyllid secondary compounds (betalaines).

Plants belonging to 26 families of the subclass Dilleniidae are fed upon by 83 lycaenid species with Ericaceae (19 species), Sterculiaceae (18), Malvaceae (10), Sapotaceae (9) and Cistaceae (8) as relatively important families. The primitive angiosperm taxa Magnoliidae (Lauraceae, Annonaceae, Piperaceae; together 17 species) and Ranunculidae (Ranunculaceae, two species) are rarely used as hosts, as are the highly advanced Asteridae (27 species on Asteraceae, but hardly any of these is specialized upon Asteraceae).

Monocots of 17 families are utilized by 36 species with Dioscoreaceae (10) and Bromeliaceae (8) prevailing, but only few of these are true monocot specialists. Rather unusual hostplants among the Lycaenidae and the butterflies as a whole are conifers (12), cycads (8), and ferns (2). The feeding habits of Liptenini (58 species feeding on lichen) and Miletinae (37 aphytophagous species) have already been discussed in detail.

Concerning the architecture of lycaenid hostplants, woody plants (trees and shrubs) and epiphytes (mistletoes) are distinctly dominant, while herbaceous plants are only utilized to some extent by the temperate zone Polyommatiti.

In all, while the subfamilies Poritiinae and Miletinae have considerably aberrant feeding habits, the hostplant pattern of the subfamilies Curetinae and Lycaeninae can be characterized by a presumably ancestral and widespread connection with Fabales and some other Rosidae families, with limited extensions towards Fagales, Urticales, Polygonales, Malvales, Ericales, and some Lamiidae groups (mainly Lamiales). Other plant taxa constitute only exceptional or occasional hosts.

The often claimed predilection of young growth and inflorescences (e.g. Pierce 1984) is well developed in the Curetinae, some Theclini subtribes, the Eumaeini and Polyommatini, but is less pronounced in the Aphnaeini and Lycaenini. Overall, this predilection of highly nutritive plant parts may thus well constitute a basic character of lycaenid hostplant use, but unfortunately this trait has been recorded rather incompletely.

An important corollary of these results is that certain plant taxa, albeit extremely diverse, rarely or never serve as hosts for lycaenid caterpillars. Such distinctly underrepresented plant taxa are Asteraceae and Orchidaceae (which are the by far largest angiosperm families in the world), further Caryophyllales, Aralianae, Theanae,

Violanae, Apocynaceae, Asclepiadaceae, Scrophulariaceae, Acanthaceae, Gesneriaceae, and all monocots. Families like Aristolochiaceae, Caryophyllaceae, Violaceae, Passifloraceae, Brassicaceae, Dipsacaceae, Campanulaceae, Cyperaceae and Juncaceae are totally absent from the current lycaenid hostplant list.

Apparently, the Lycaenidae with their specialization towards the Rosidae had limited success in colonizing these latter plant groups that are mostly characterized by peculiar secondary compounds. Although direct evidence is missing, this suggests that chemical barriers have played a major role in the evolution of hostplant relationships within the Lycaenidae. Host shifts occurred most often among taxonomically or chemically related plants, or while specializing on plant tissues rather poor in secondary compounds (e.g. young unexpanded foliage).

Indeed, polyphagy of many lycaenids is strongly correlated with specialization on young foliage or inflorescences, suggesting that "oviposition errors" under such circumstances provided important opportunities for amplifying the host range (Chew & Robbins 1984). Harvey (1987) noted a similar trend towards polyphagy in Riodinidae caterpillars utilizing extrafloral plant nectar.

This generalized view of Lycaenidae hostplant relationships is partly obscured by the characteristic and highly diverse hostplant relationships of many of the subordinated taxa (see above). Most likely this is due to adaptations of these taxa to cope with the secondary compounds of their respective hostplants.

In this respect the lycaenids are typical herbivores and pronouncedly resemble the butterfly families Papilionidae, Pieridae and Nymphalidae, where typically subfamilies, tribes or genus-groups all share basic hostplants, although numerous secondary deviations do occur (e.g. Ackery 1988). A general reservation of the patterns described here is that the available database considers only one fourth of the extant species diversity of the Lycaenidae.

Lycaenid hostplants in comparison to other butterflies

Ehrlich & Raven (1964) have already noted that the hostplant ranges of Nymphalidae and Lycaenidae apparently show little overlap. On the grounds of Ackery's recent treatise (1988) and the data compiled in the Appendix, this notion can now be investigated more precisely.

Nymphalids indeed heavily utilize plant taxa that play little or no role as lycaenid hosts. Monocots (mainly Bromeliales, Cyperales, Poales, Arecales) are the typical hosts of Brassolinae, Amathusiinae, Satyrinae, and several Morphinae. Acraeinae predominantly feed on Violanae and Urticales; Heliconiinae on Passifloraceae; Argynninae on Violales; Melitaeinae on Scrophulariaceae and Asteraceae; Nymphalinae, Apaturinae and Libytheinae on Urticales; Danainae on Asclepiadaceae and Apocynaceae; and Ithomiinae on Solanaceae.

Only some *Morpho* species and, in part, the subfamilies Charaxinae and Limenitinae show some overlap with the Fabales or, more generalized, with the Rosidae theme so typical for the Lycaeninae.

This gross pattern provokes an evolutionary interpretation, and I here present two ideas that may stimulate, but not anticipate, a more detailed discussion. First, the general Rosidae theme of the Lycaeninae could indicate that these butterflies and the Rosidae diversified in parallel. The Rosidae are an assemblage of moderately advanced dicots that mainly evolved during the late Cretaceous and early Tertiary, and from zoogeographical reasons the principle divisions of the Lycaenidae occurred in this same period.

In this scenario, the Lycaenidae basically maintained and diversified while pertaining their primary association with Rosidae families (notably legumes). They only sporadically managed to shift to unrelated lineages, most likely in the presence of chemical similarities. This "parallelism in time scenario" could explain why lycaenids do rarely feed on either ancestral (Magnoliidae) or advanced angiosperms (Asteridae, many monocots).

A second and by no means mutually exclusive scenario invokes competition. Nymphalids, starting from their possibly primary association with Urticales (Libytheinae, Nymphalinae), successfully colonized the modern angiosperm taxa (Dilleniidae, Lamiidae, Asteridae, monocots) and occupied many potential niches for butterfly caterpillars, thus preventing a more extensive shift of lycaenids onto these plants. This "competition scenario" implies that nymphalids have derived their remarkable diversity through considerably effective mechanisms to cross the chemical barriers imposed by secondary plant compounds.

A comparison of Papilionidae hostplants with the lycaenid pattern likewise yields distinct differences. Papilionids heavily utilize Magnoliidae (e.g. Lauraceae, Annonaceae, Aristolochiaceae), suggesting an ancient association with primitive angiosperms. This well matches the systematic position of the Papilionidae as the most primitive family of true butterflies. The basic radiation of papilionids certainly predates that of lycaenids.

Furthermore, advanced Papilioninae (*Papilio* in part) have specialized on resiniferous plants (Rutaceae, Apiaceae). Both the ancient and the more modern papilionid hostplant groups bear little importance for caterpillars of the Lycaenidae. An interpretation of the association of the primitive monobasic papilionid subfamily Baroniinae with legumes is currently impossible.

Pieridae larvae feed on legumes and other Rosidae (Loranthaceae, Rhamnaceae: Dismorphiinae, Coliadinae), as well as on Capparales (many advanced Pierinae). The latter plants contain highly characteristic secondary compounds (glucosinolates etc.) and have never been reported to be utilized by lycaenid caterpillars.

The considerable overlap of ancestral Pieridae and Lycaenidae hostplants suggests that their last common ancestor might have lived on legumes. Possibly, the basic radiations of Pieridae and Lycaenidae occurred at the same time ("parallelism in time scenario"), with one pierid group later successfully colonizing a novel type of hostplants.

The hostplants of Riodinidae are rather sketchily known and cover a broad array of at least 46 dicot and monocot families (Harvey 1987). A general pattern is not yet ap-

parent, although several subfamilies or tribes have characteristic hostplant relationships. Riodinid caterpillars do not predilect young foliage or inflorescences of their hostplants, thus differing distinctly from many lycaenids.

In summary, confirming the view of Ehrlich & Raven (1964), there is only limited overlap in the patterns of hostplant use between the Lycaenidae, and the remaining butterfly families Papilionidae, Pieridae, Nymphalidae and Riodinidae. The only significant congruence between the pierid subfamilies Dismorphiinae and Coliadinae, and Lycaenidae suggests a common ancestral association of these two families with the Rosidae and especially with legumes.

The characteristic differences among the hostplant patterns of the butterfly families can be tentatively related to historical coincidences of major steps in angiosperm evolution with basic radiations of the respective butterfly taxa, as well as to sequences of occupation of potentially available hostplant taxa. Clearly, these topics requires a more thorough analysis beyond the scope of the present study.

Are there trade-offs with myrmecophily?

In the preceding paragraphs three generalized results have crystallized out: not surprisingly, most lycaenid subfamilies, tribes or subtribes possess taxon-characteristic hostplant-relationships; there is indeed an overall association of phytophagous lycaenids with the plant subclass Rosidae and especially the order Fabales, as well as a predilection for young foliage or inflorescences; and, the hostplant pattern of Lycaenidae shows only limited overlap with the remaining butterfly families. These findings shall now be related to myrmecophily.

At first glance the overall lycaenid pattern appears to support the "preference hypothesis", according to which myrmecophilous lycaenids should preferably feed on protein-rich plants such as Fabales or Santalales (Pierce 1985). However, several objections qualify this view.

First, legumes appear to be the ancestral hostplants of the Lycaenidae and are fed upon by the primarily myrmecoxenous Curetinae as well as by rather old Pieridae lineages. In the latter family, there are no certain records of true myrmecophily, and the few reports of ants visiting the secretory setae of young pierid caterpillars predominantly involve species feeding on non-legumes (e.g. Brassicaceae).

Secondly, within the myrmecophilous subfamily Lycaeninae the connection with legumes is widespread, but by no means ubiquitous. Myrmecophilous taxa like Luciiti, Arhopaliti, Catapaecilmatiti, Amblypodiiti, Loxuriti and Hypolycaeniti show only very weak associations with Fabales or Santalales at most.

Thirdly, even in such taxa with a general Fabales theme (Aphnaeini, Zesiiti, Deudorigiti, Eumaeiti, Polyommatini) a considerable portion of the myrmecophiles does not utilize legumes as larval food (e.g. 48 % in the Aphnaeini, 46.5 % in the Polyommatini).

Fourthly, mistletoe-feeders generally do not show a pronounced state of myrmecophily. While the few Ogyriti species are all myrmecophilous, the by far more species-rich Iolaiti apparently exhibit a lower level of myrmecophily, and ant-associations are

unknown from several mistletoe-feeders in other taxa (Eumaeiti: *Atlides, Callophrys*). In all, only about one half of the ant-associated Lycaenidae caterpillars feed on legumes or mistletoes, while the other half utilize a broad range of plants including ferns, cycads, or monocots.

Furthermore, there is no indication that obligatorily myrmecophilous lycaenids show a more close association with legumes than their facultatively ant-associated counterparts. If legumes were really that important for maintaining ant-associations, one should expect that obligatory myrmecophiles do pronouncedly predilect these plants. Within the Aphnaeini, however, the proportions of legume-feeders among obligate and facultative myrmecophiles are nearly identical, and within the Polyommatini the pattern is even reversed. In this tribe the majority of obligate myrmecophiles do not feed on legumes.

Finally, nitrogen-fixation is not restricted to the Fabales, but occurs in several families of the Hamamelididae (Betulaceae, Myricaceae, Casuarinaceae), Rosidae (Rosaceae, Rhamnaceae, Coriariaceae, Elaeagnaceae), and Dilleniidae (Ericaceae), always by means of symbioses with actinomycete fungi (Ehrendorfer 1983).

All these families are found in the hostplant list of lycaenid caterpillars, but only from three of the 13 lycaenid species, that reportedly feed on the genera known to have such fungus-symbioses, ant-associations have been recorded (*Hypochrysops piceatus, Celastrina argiolus, Lycaeides idas*).

These objections do not truly invalidate the preference hypothesis in total. In fact, it is well conceivable that the association of ancestral Lycaeninae with legumes provided an important nutritional preadaptation for these butterflies to enter into mutualistic associations with ants based on trophic secretions.

Experimental evidence also supports the notion that the quality of larval nutrition may be decisive for the maintenance of myrmecophily (Fiedler 1990c, Baylis & Pierce 1991). Rather, the above arguments indicate that starting from their primary association with legumes, roughly one half of the myrmecophilous lycaenids have successfully increased or even entirely shifted their hostplant range, but still maintain their symbiotic relationships towards ants.

Obviously, myrmecophilous lycaenid caterpillars were able to specialize on novel hostplants in evolutionary time, and, given the large diversity of hostplants of myrmecophilous lycaenids, there is no evidence that ant-associations have provided a powerful selective force preventing or channelling hostplant shifts.

In one respect, however, the preference hypothesis generally holds true: secondary myrmecoxeny is much more common in species not feeding on legumes, this difference being statistically significant in the Theclini, Deudorigiti, and Polyommatini. Thus, shifts towards "nutritionally inferior" hostplants enhance the likelihood of reducing ant-associations, whereas on legumes the ecological conditions have more rarely favoured the step towards secondary myrmecoxeny (see last chapter).

The second hypothesis concerning lycaenid hostplant patterns and myrmecophily predicts an amplified host range in response to associations with specific ants (Pierce

& Elgar 1985). Based on the results presented above, this trait is extremely instable across the higher lycaenid taxa.

Among the well-known Aphnaeini and Polyommatini there is no indication that myrmecophiles have a wider host range than myrmecoxenous species, or that obligate myrmecophiles are more polyphagous than facultative ones. Overall, 75 % of the Aphnaeini and Polyommatini are oligophagous (i.e. restricted to one hostplant family) with no respect of their degree of myrmecophily.

In contrast, there is a statistically significant difference in the degree of polyphagy between myrmecophiles and non-myrmecophiles within the Theclini and Eumaeini. The majority of polyphagous Theclini (a similar result was obtained for the Luciiti alone) are usually myrmecophilous, as are polyphagous members of Old World Eumaeini tribes (this trend is particularly prevalent in the Deudorigiti). In contrast, most myrmecoxenous Theclini and Eumaeini species are food specialists. Astonishingly, the degree of polyphagy does not differ between obligatory and facultative myrmecophiles among the Theclini (same result obtained for Luciiti alone), and within the Old World Eumaeini obligate and specific myrmecophiles are almost unknown.

Hence, it is very unlikely that the polyphagy of quite a number of Theclini and Eumaeini caterpillars has evolved in response to specific ant-associations. If this were the case, the widest host ranges were to be expected among those lycaenids obligatorily associated with particular host ants. This does clearly not apply to the Deudorigiti, at least.

Furthermore, less than 25 % of the species of both tribes are reportedly polyphagous. So, polyphagy in the Theclini and Eumaeini may only in single instances really be related to obligatory and specific ant-associations. Rather, the physiological potential to utilize a wide hostplant range (usually via flower or fruit-feeding) appears to be a characteristic trait of certain genera (e.g. *Hypochrysops, Arhopala, Hypolycaena, Deudorix, Rapala*), and only within groups thus phyletically preadaptated the relative importance of ants as oviposition cue could secondarily override the generally leading role of plant chemistry (e.g. *Hypochrysops ignitus, H. miskini, H. apelles, Arhopala centaurus, A. pseudocentaurus, Hypolycaena phorbas, H. erylus*).

The relative over-representation of oligophagous species among myrmecoxenous Theclini might be due to the trend outlined above that myrmecoxeny is more likely to evolve on "nutritionally inferior" hostplants. Lauraceae, Moraceae (*Philiris*), Fagaceae and related Hamamelididae families (Thecliti) are rather untypical lycaenid hostplants whose colonization supposedly required appropriate physiological specializations.

At the same time these plants may well represent such inferior hostplants that, in concert with other ecological factors (e.g. low ant abundance in canopies of temperature zone Fagaceae forests), have favoured the reduction of ant-associations. In addition, oligophagous caterpillars are generally subject to a lower selective pressure arising from predation (Bernays 1988, Bernays & Cornelius 1989), and this alternative "defense" may further have limited the selective advantage of low-level myrmecophily.

Myrmecoxenous Eumaeini often exhibit another type of alternative defense, namely endophytism, which in combination with monophagy apparently furthered the reduction of myrmecophily (e.g. *Artipe eryx, Bindahara phocides, Capys*).

The myrmecoxenous genus *Eumaeus* even feeds on cycads containing toxic secondary compounds (e.g. cycasine), and its gregarious aposematic caterpillars have been shown to be unpalatable to ants and birds due to the sequestering of these allelochemicals (Bowers & Larin 1989, Bowers & Farley 1990).

In summary, the general hostplant pattern of lycaenid caterpillars seems to be governed by the same principles as in other Lepidoptera taxa: chemical barriers and adaptations to overcome these, availability of potential hostplants in space (i.e. geographic range) and time, and possibly competition and resource partitioning among the major butterfly lineages.

As a consequence, the hostplant pattern of the Lycaenidae shows distinct relationships to phylogeny and systematics, and the consideration of these relationships is crucial. There is little evidence for consistent trade-offs between hostplant preferences and myrmecophily across the whole diversity of the Lycaenidae, suggesting that in evolutionary time lycaenid caterpillars were able to maintain ant-associations even on unusual hostplants, and thus limiting the explanatory or predictive validity of the preference and the amplified host range hypothesis proposed by Pierce (1985) and Pierce & Elgar (1985), respectively.

Significant trade-offs do however exist between the evolution of secondary myrmecoxeny and the association with non-legume hostplants. A universal correlation between hostplant range and myrmecophily does not exist, and in the cases where ant-dependent oviposition coincides with polyphagy, this is usually based on rather catholic feeding habits of the whole taxonomic group in question.

ZOOGEOGRAPHY OF LYCAENID-ANT INTERACTIONS

Zoogeography of the Lycaenidae

Only one work (Pierce 1987) has previously dealt with the zoogeographical aspects of myrmecophily within the Lycaenidae. The main conclusion of Pierce was that myrmecophily is much more common in the southern hemisphere, with 70—90 % of all lycaenids being ant-associated, than in the northern hemisphere, where myrmecophily was stated to occur in less than one third of the species.

In addition, obligate ant-associations were found to be widespread in the southern hemisphere, whereas in the Holarctic region less than 10 % of the lycaenids are obligatorily myrmecophilous.

Thus, the proportion of myrmecophilous lycaenids and the obligateness of their ant-associations were postulated to show a clear north-south disparity. Pierce (1987) emphasized that this disparity should neither be due to any peculiarities in the distribution of myrmecophily among the lycaenid taxa, nor to the different geographical distributions of the lycaenid taxa themselves.

However, since in the preceding chapters significant interrelationships between lycaenid systematics, the larval hostplant patterns, and the occurrence and specificity of myrmecophilous associations have been disclosed, it seems worthwhile to search for such correlations between systematics, zoogeography, and myrmecophily as well.

Furthermore, the higher classification underlying the study of Pierce (1987) still contained, among others, the "Theclinae" sensu Eliot (1973), and these are now known to be a paraphyletic assemblage. The use of paraphyletic or polyphyletic units may well have masked important evolutionary traits.

In addition, the figures given by Pierce (1987) concerning the proportion of myrmecophilous lycaenids in the western Palaearctic region have recently been questioned on the grounds of an extensive literature survey (Fiedler 1991). Therefore, the whole complex of zoogeographical implications on myrmecophily will here be carefully re-examined within the systematic framework of the preceding chapters.

As a first step, the zoogeography of the higher lycaenid taxa has to be reviewed briefly. Eliot (1973) was the first to discuss the global zoogeography of the Lycaenidae using his systematic approach, and the reader is referred to his work for numerous further details and references (see also Stempffer 1967).

The main aim of this first part of the analysis is to investigate whether the higher lycaenid taxa have characteristic distributional patterns that may affect the faunal composition in the different zoogeographic regions. In the second part of this chapter, the systematic structure of the lycaenid faunas and their proportions of myrmecophilous species will be examined using 8 selected regions. Finally, I will attempt a synthesis of these data on systematics, zoogeography, and myrmecophily.

Poritiinae

This second-largest lycaenid subfamily is entirely restricted to the Old World tropics and subtropics. It further divides into two tribes with characteristic distributions. The Oriental Poritiini comprise about 50 species that occur solely in India, South East Asia and the Indonesian archipelago. The Ethiopian Liptenini with more than 500 species (Stempffer 1967), in contrast, are confined to Africa south of the Sahara desert with main diversity in tropical central Africa.

The Liptenini further subdivide into three subtribes one of which, viz. the Durbaniiti, is a small and basically southern African taxon of more xeric habitats (perhaps a specialized lineage derived from Lipteniti-like ancestors). The Pentiliti are distributed throughout Africa south of the Sahara with some 130 species, while the most advanced Lipteniti (more than 380 species) are mainly tropical.

There is evidence that the two Poritiinae tribes are sister-groups, although their evolutionary history is not well understood. Poritiinae larvae are basically myrmecoxenous, with only some Lipteniti exhibiting relationships towards ants that are supposed to represent commensalism. Nevertheless, the largely myrmecoxenous Liptenini account for a siginificant proportion (about 35 %) of the African lycaenid fauna. The Poritiini only weakly contribute to the diversity of the Oriental Lycaenidae (e.g. 6 % in Thailand, Peninsular Malaysia, and Borneo).

Miletinae

This rather small subfamily (about 140 species) is essentially confined to the Old World tropics as well, but it weakly extends into northern Australia, the eastern Palaearctic and the Nearctic region with one species each. The Australian and Japanese populations of *Liphyra brassolis* and *Taraka hamada*, respectively, have clearly secondarily invaded from South East Asia, which is the main distributional area of both species.

The Nearctic endemic *Feniseca tarquinius*, in contrast, may either represent an old Tertiary relic of a former Holarctic subtropical Miletinae fauna that was subsequently eradicated in the Palaearctic through the glaciations. Or, coming from eastern Asia, it may have entered America via the Bering strait. Anyway, the main stock of the Miletinae is clearly African and Oriental.

The two tribes Miletini and Liphyrini show a less sharp geographical disjunction than the two Poritiinae tribes. The Miletini are predominantly Oriental (about 75 species). Only the genera *Megalopalpus* (Miletiti) and *Spalgis* (Spalgiti) occur in Africa with less than 10 species together.

The Lachnocnemiti (included into the Miletini by Scott & Wright 1990, but more likely the sister-group of the Liphyrini: Eliot, pers. comm.) are entirely African (35 species), as are the Liphyrini (20 species) with the only exception of *Liphyra*.

The Miletinae everywhere constitute a minor component of the lycaenid fauna at most (8 % in southern Africa as well as in Thailand and Peninsular Malaysia, 11 % in Borneo).

Curetinae

The myrmecoxenous Curetinae (18 species) are confined to the Oriental region with one species extending into the eastern Palaearctic (*Curetis acuta*) and another occurring in New Guinea and adjacent archipelagos (*C. barsine*; Eliot 1990). Even in the area of their main diversity (Sundaland), the Curetinae do never build up more than 2 % of the lycaenid fauna.

Lycaeninae

This huge subfamily has a cosmopolitan distribution, but its tribes and subtribes again exhibit peculiar geographical patterns.

a) Aphnaeini

This tribe is basically confined to the Ethiopian realm. Only about a dozen species of the genus *Spindasis* occur in the Oriental region with a single representative extending as far northeast as Japan (*S. takanonis*).

Another and rather closely related lineage (*Cigaritis* including *Apharitis*), comprising a further dozen of species, is essentially eremic, reaching the southwestern Mediterranean area and extending through Arabia and the Middle East to the deserts of Central Asia.

The remaining 230 Aphnaeini species nearly exclusively occur in Africa south of the Sahara and constitute a significant component of the African lycaenid fauna (16 % of the whole African species diversity, but more than 36 % in southern Africa).

b) Lycaenini

This small tribe with less than 100 species provides a zoogeographical enigma (cf. Eliot 1973). The majority of species are Holarctic (genus *Lycaena* s. l.). A couple of *Lycaena* species occur in eastern Africa and have even reached South Africa, possibly having invaded through the East African mountains. Four additional *Lycaena* species are endemic to New Zealand, and their history remains a mystery.

The second phyletic lineage among the Lycaenini is the *Heliophorus* section, and this is largely an Oriental group with one genus (*Melanolycaena*) being confined to New Guinea (Sibatani 1974), while the single species of *Iophanus* is restricted to the mountains of Guatemala. The isolated occurrence of Lycaenini in New Zealand and Central America poses a challenge to zoogeography.

Irrespective of this, the largely myrmecoxenous Lycaenini contribute only 10-15 % to the species diversity of the Lycaenidae in the Holarctic realm and considerably less elsewhere.

c) Theclini

The Theclini sensu Scott & Wright (1990) are restricted to Eurasia and Australia with only 2 small Thecliti genera (*Habrodais, Hypaurotis*) occurring in North America. Two subtribes, Luciiti and Ogyriti, are entirely Austro-Melanesian (one Luciiti species, *Hypochrysops coelisparsus*, reaches South East Asia: Sands 1986). The third subtribe Zesiiti is also mainly Australian with the exception of the Indian *Zesius chrysomallus*.

The largest subtribe are the Oriental Arhopaliti with weak extension into New Guinea, northern Australia and the south-eastern Palaearctic. The fifth subtribe Thecliti is Sino-Oriental, but is also weakly represented in the western Palaearctic and Holarctic region and in South East Asia.

The basically myrmecophilous Theclini subtribes play major roles in the faunal composition of Australia (47 %) and South East Asia (ca. 30 %), while the largely myrmecoxenous Thecliti are important in the eastern Palaearctic region (e.g. 40 % in Japan). In all, the Theclini as a whole as well as its subtribes exhibit peculiar distributional patterns.

d) Eumaeini

This tribe is nearly cosmopolitan, but again its subtribes show very distinctive distributions. Catapaecilmatiti, Loxuriti, and Remelaniti (in the delimitations of the systematic chapter, see above) are strictly Oriental. Amblypodiiti, Iolaiti, Hypolycaeniti, and Deudorigiti are Oriental and African, Oxyliditi are African, and Hypothecliti are Papuan. There is some reason to assume that the Oriental members of the Iolaiti (and possibly those of the Hypolycaeniti and Deudorigiti as well) are derived from invaders from an old African stock (Eliot 1973).

The remaining and largest subtribe Eumaeiti is primarily Neotropical with only about 110 species in the Holarctic compared to an estimated 1000 species in the Neotropics (Bridges 1988, Robbins, pers. comm.). The North American Eumaeiti largely belong to the genera *Satyrium* and *Callophrys* s. l., and the Palaearctic representatives (ca. 55 species) are clearly derived from rather late invaders of the latter two genus groups via the Bering route.

e) Polyommatini

The Polyommatini are represented on all continents except Antarctica, but as with the Eumaeini their subgroups show distinctive patterns. Candaliditi are entirely Austro-Melanesian, Lycaenesthiti are African with weak secondary representation through the Oriental region including northern Australia, and Niphanditi are Oriental with one Palaearctic extension.

Polyommatiti are most strongly represented in Africa (*Cupidopsis, Uranothauma, Leptotes, Castalius, Zizeeria*, and *Euchrysops* sections are mainly African), the Oriental region (*Nacaduba, Jamides* and *Lycaenopsis* sections have their headquarters there), and the Palaearctic realm (*Everes, Glaucopsyche*, and *Polyommatus* sections).

The diversity of New World Polyommatini is surprisingly poor. The American members of the *Everes, Lycaenopsis, Glaucopsyche*, and *Polyommatus* sections are probably all derived from rather late invaders from Asia across the Bering route. Only the small aberrant *Hemiargus* group of genera within the *Polyommatus* section is truly American with less than 30 species (Nabokov 1945).

Eliot (1973) assumes that this *Hemiargus* group represents an earlier invasion across the Bering strait, and this agrees rather well with the today distribution of some of its members (cool-temperate mountainous Andine habitats). The isolated occurrence of

single members of the mainly African genera *Leptotes, Brephidium*, and *Zizula* is probably best explained by waif dispersal across the Atlantic ocean (Eliot 1973).

In summary, Africa and South Asia house the most diverse lycaenid faunas with respect to the presence of higher taxa (subfamilies, tribes, subtribes). The oldest lineages are today confined to the Old World tropics. The Palaearctic region has a comparatively depauperate fauna due to the repeated glaciations, and Australia's lycaenid fauna is rich in endemics (even on subtribal level), but rather poor in species diversity.

Most strikingly, the New World lycaenid fauna is very homogeneous. The Neotropical fauna consists almost entirely of members of one single subtribe, and the Nearctic fauna is largely derived from rather young Asian or Neotropical invaders. Apparently, the early and long-lasting isolation of North America precluded the evolution of a diverse autochthonous lycaenid fauna, and the Neotropics were primarily colonized by only one, albeit extremely speciose lineage, viz. Eumaeiti.

Obviously the distribution of the higher lycaenid taxa is far from being uniform, thus contradicting the conclusion of Pierce (1987) that the zoogeography of the Lycaenidae is largely independent of their phylogeny. In contrast, most higher lycaenid taxa as recognized throughout this work have distinctive distributions, and the systematic structure of the lycaenid faunas of all biogeographical realms investigated is indeed significantly shaped by these differences.

Since the higher taxa also have characteristic traits with regard to myrmecophily (see above), the faunal composition heavily influences the distribution and degree of myrmecophily in the various regions.

Zoogeographic patterns in lycaenid myrmecophily

Introductory remarks

In this chapter I will discuss the systematic structure, and the proportions of myrmecophilous species, of the lycaenid faunas of eight selected regions (viz. Europe and North West Africa, Japan, Australia, West Malaysia and Thailand, India, South Africa, North and South America). Except West Malaysia/Thailand and the Neotropics, these regions are the same as analysed by Pierce (1987), allowing direct comparisons with her data and conclusions.

From all of these regions, with the exception of the Neotropics, the faunistic knowledge of the Lycaenidae is sufficient to permit rather definite conclusions regarding approximate species diversity and systematic faunal structure. Despite the poor systematic and ecological knowledge, the Neotropics were included since they constitute a species-rich major biogeographical region for their own.

Therefore, all biogeographical realms are represented in the following analysis, although the Eastern Palaearctic and Neotropics strongly require a more thorough discussion on the grounds of more detailed faunistic and ecological information. The unevenness of the faunistic treatments and associated problems are discussed in the respective paragraphs.

Pierce (1987) performed comparisons between the regions using both the numbers of species and genera. Here I only focus on the analysis of species numbers on twofold reasons. First, as a theoretical argument, the species (as groups of populations maintaining genetic exchange) are the units that are subject to evolutionary processes such as selection or genetical drift.

Genera and higher taxa, in contrast, are historical entities at best (in the case of a truly phylogenetic system), or simply arbitrary assemblages (in the case of para- or polyphyletic taxa). Even monophyletic higher taxa are, however, not subject to ecological or evolutionary processes acting in phenomena like myrmecophily.

Accordingly, comparative analyses within higher taxa are appropriate to elucidate general trends and patterns of ecological phenomena like myrmecophily (see above), whereas simple numerical comparisons between higher taxa yield doubtful results, in particular when paraphyletic units are involved. At least, such quantitative analyses should incorporate the information content of the underlying hierarchical phylogenetic system (e.g. the concept of "taxic diversity": Vane-Wright et al. 1991).

Secondly, as a more practical argument, the use of lycaenid genera in any ecological and evolutionary considerations is precluded by the extremely uneven use of generic concepts among the different systematic approaches. This is mainly due to the preponderance of typological instead of phylogenetic systematics in the treatment of most butterfly groups.

Some examples may illustrate the associated difficulties. Higgins & Riley (1978) divided the European coppers (Lycaenini) into four genera (other authors even use seven genera). Kudrna (1986), in contrast, retained all these species in the single genus *Lycaena*. In North America, the coppers are likewise treated as one genus *Lycaena* by Scott (1986), whereas other authors subdivide the same group of 15 species into seven genera (Bridges 1988).

While *Lycaena* is probably a monophyletic taxon, most of the atomized "genera" are not based on synapomorphies, but simply reflect typological affinities. Furthermore, the exclusion of small, derived species-groups from larger, monophyletic genera often renders the remaining assemblage of species paraphyletic.

A parallel case is the generic treatment of the Holarctic *Polyommatus* group. Scott (1986) lumped all North American species into *Plebejus*, while Higgins & Riley (1978) splitted the European representatives into no less than 14 "genera".

Apart from all problems regarding the monophyly of the resulting taxa, it is obvious that such an unevenness must necessarily affect quantitative analyses based on different generic concepts. Pierce (1987), for example, used Higgins & Riley (1978) and Scott (1986) as taxonomic sources for Europe and North America, respectively. Thus, applying Scott's generic concept to the *Lycaena* and *Polyommatus* groups alone would have reduced the number of European lycaenid genera from 43 to 27. *Vice versa*, the result would be an increase of North America's genus number from 39 to at least 49.

Comparisons on genus level can only be useful if the generic concepts are harmonized, and this is at present impossible for the Lycaenidae fauna under a global view. Restric-

ting the following analyses to the species level still retains a number of unresolved taxonomic problems (species *versus* subspecies, sibling species etc.), but these seem more tolerable for the purpose of this chapter.

The quantitative analyses were conducted in the following way. First the complete lycaenid fauna of each selected region (except the Neotropics) was assessed using available faunistic literature, and rearranged according to the system used throughout this work.

Secondly, all species occurring in one region, for whom ecological information is available, were selected and the definite species records of myrmecophily were counted, with obligate myrmecophily being treated separately wherever possible. Doing so, I evaluated all information available for any species with no respect of the particular geographic area in question (database see Tab.17 in the Appendix).

For example, *Leptotes pirithous* was designated as facultatively myrmecophilous using African records in the analysis of Europe as well, although I have no European records of ant-associations for this species. There is at present no published evidence that some populations of one lycaenid species are myrmecophilous, while other populations of the same species are myrmecoxenous. Less pronounced interpopulation differences in the degree or specificity of myrmecophily, however, are likely to occur and are worth being documented.

This step of the analyses yielded the number of species with ecological information present and its assured minimum proportion of facultative and obligate myrmecophiles (the first three columns in the tables of the following paragraphs).

In a third step, the analyses were extended to the whole species diversity of the respective regions, using conservative myrmecophily estimates based on close relatives for all those species where no definite information is available (the latter three columns in the following tables).

This procedure is validated by the distinct correlations found between myrmecophily and systematics (see above) as well as by the similarity of the results obtained for the European fauna using this "indirect" method when compared with the direct evidence (see below). The results of both approaches are then compared with those of Pierce (1987).

Europe and North West Africa

The zoogeographical implications on myrmecophily in this part of the Western Palaearctic have been discussed in detail by Fiedler (1991). Therefore, these results shall be only briefly summarized here to facilitate further comparisons. The lycaenid fauna of Europe and North West Africa (delimitations following Higgins & Riley 1978) is taxonomically and ecologically rather well known, although for several species not even the hostplants have been recorded.

Ecological data are present for the immatures of 107 species, 68 of which (63.5 %) are surely known to be ant-associated including 10 (9.3 %) obligate myrmecophiles. The

whole fauna comprises 116 species (largely based on Kudrna 1986), of which an estimated 91 species (78.4 %) are most likely myrmecophilous including 10 (8.6 %) obligate myrmecophiles.

These figures contradict sharply to the results of Pierce (1987) who found a proportion of myrmecophiles of only 30.4 %. This difference has three main reasons. First, Pierce (1987) evaluated only a small list of references (largely the review papers of Hinton 1951, Malicky 1969b, and Kitching & Luke 1985, as well as identification guides such as Higgins & Riley 1978) and hence overlooked a number of records published in numerous faunistic or ecological reports.

Secondly, considerable progress has been made in recent years in the investigation of lycaenid myrmecophily in the Western Palaearctic, in particular in Spain and North West Africa (e.g. Munguira & Martín 1988, 1989a, b, Rojo de la Paz 1990). When compiling my database, I attempted to utilize all such sources exhaustively, including personal communications of several colleagues.

And thirdly, Pierce (1987) totally neglected the systematic component. Accordingly, she designated all species as "not myrmecophilous" in the absence of positive records. This procedure has been refuted in a number of cases where recent research has proven the existence of ant-associations, and it certainly results in a severe underestimate for the proportion of myrmecophiles in all other zoogeographical regions as well.

Given that at least more than 60 % (and most likely more than three quarters) of the European lycaenids are ant-associated, the question arises as to whether there is a systematic pattern involved. This is indeed the case.

In the Western Palaearctic, all lycaenids belong to the primarily myrmecophilous subfamily Lycaeninae, and the vast majority of species (72.4 %) are Polyommatini. In this latter group only very few species are definitely secondarily myrmecoxenous (six *Agriades* and *Vacciniina* species in the *Polyommatus* group). In addition, all of the five Aphnaeini species and seven of the European Eumaeiti species are certainly or most likely myrmecophilous.

Only the Lycaenini are a basically myrmecoxenous tribe with 13 representatives. Thus, the preponderance of one single myrmecophilous tribe alone accounts for the majority of myrmeophiles among the European lycaenids, whereas only one myrmecoxenous tribe comprises about one half of the rather few myrmecoxenous species.

Another interesting biogeographical result is a north-south gradient in the proportion of myrmecophilous species. Lycaenid species diversity increases distinctly from the North Cape towards the Mediterranean region and declines again towards the Sahara desert. The proportion of myrmecophilous species, in contrast, increases asymptotically from one third in the subarctic areas to roughly 80 % throughout the Mediterranean area and North Africa. South of 55 ° northern latitude the proportion of ant-associated species is consistently higher than 75 %, while only north of 65 ° this proportion is well below 60 %.

In other words: the proportion of myrmecophilous species does not differ substantially between the Mediterranean area and Central Europe. Pierce (1987) could not find a

Tab.10: Faunal composition and myrmecophily of European and North West African Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	-	-	-	-	-	-
Curetinae	-	-	-	-	-	-
Lycaeninae	107	68	10	116	91	10
Aphnaeini	4	4	3	5	5	3
Lycaenini	10	0	0	13	0	0
Theclini	3	1	0	3	1	0
Eumaeini	11	6	0	11	7	0
Polyommatini	79	57	7	84	78	7
Lycaenidae	107	68	10	116	91	10

similar gradient between tropical and temperate areas in Australia, nor between subtropical and temperate areas of Japan. This suggests that climatic effects on myrmecophily become important only in high latitudes. In Europe, this obviously applies only to the northernmost boreal forests and the subarctic tundra.

At least three factors have probably shaped this gradient:

— First, the ant fauna of subarctic and northern boreal areas is extremely impoverished (Hölldobler & Wilson 1990, Heinze, pers. comm.). Thus, the chance of maintaining ant-associations and its related selective advantage is very low and, accordingly, myrmecophilous lycaenids have only the costs of developing ant-organs, but receive little, if any benefits.

— Secondly, the lack of appropriate ant partners may have limited or inhibited the recolonization of the subarctic region by myrmecophilous lycaenids after the glaciations.

— And thirdly, the short vegetation period in combination with limited nutritional resources may pose severe constraints to the production of energy-rich myrmecophilous secretions by lycaenid larvae.

A depauperate ant fauna and a shortened vegetation period are also characteristic for high altitude biomes. Interestingly, studies on altidudinal effects on Neotropical mutualisms between ants and plants (Koptur 1985) or membracids (Olmstead & Wood 1990b) revealed a distinct decrease of the number and proportion of ant-associations with increasing elevation. High-altitude membracids in South America are mostly not ant-associated, and plants bearing extrafloral nectaries may use alternative defense strategies there. Likewise, myrmecophily in the Neotropical Riodinidae is restricted to species of lower habitats (DeVries, pers. comm.).

Appropriate data for lycaenids are missing, but a preliminary survey of lycaenids in the Alps failed to detect significant differences in the altidudinal distribution of myrmecophilous versus myrmecoxenous lycaenids (Fiedler, unpublished). Detailed ecological studies on the degree of myrmecophily of species occurring at a wide range of altitudes would be rewarding. Furthermore, faunal surveys of mountain areas with a greater range of altitudes and a more diverse lycaenid fauna may demonstrate such altitudinal gradients in myrmecophily. At present, the available data are too scanty to allow appropriate analyses.

Overall, the lycaenid fauna of the Western Palaearctic is characterized by a high proportion of myrmecophilous species, a rather low number (< 10 %) of obligate myrmecophiles, and the preponderance of one single myrmecophilous subtribe (Polyommatiti; see Fiedler 1991).

Japan

The lycaenid fauna of Japan comprises 61 species in three subfamilies. Due to the intensive work of numerous lepidopterists, the distribution and ecology of Japanese lycaenids is exceedingly well known. The life-histories of all species have been recorded, although a number of reports on larval biologies result from laboratory breedings only.

Accordingly, the knowledge of myrmecophily is still rather fragmentary. As a major source I utilized Shirôzu & Hara (1974), supplemented by a number of journal articles (e.g. Iwase 1953, 1954, 1955, Wakabayashi & Yoshizaki 1967, Ejima et al. 1978, Matsuoka 1978, Hama et al. 1989). For some species, information from outside Japan was used as well.

Twenty-seven of the 61 species (44.3 %) are surely known to be myrmecophilous, and seven further species are strongly suspected to be ant-associated as well. Thus, probably 55.4 % of the Japanese lycaenids are myrmecophilous. Only 5 or 6 species (8.2—9.8 %) maintain obligatory relationships to ants.

These figures again contrast distinctly with those given by Pierce (1987). However, the interpretation of her results is further complicated by inconsistencies within this latter paper. In her Tab.1, Pierce states that 14 out of 62 species (22.6 %) are myrmecophilous, while in Tab.2 and Figure 1, 25 out of 72 (!) species (34.7 %) are given as ant-associated. Reasons for the different total species numbers are not apparent (possibly a printer's error?), nor are the divergent myrmecophily data explained.

Given that the total species number of Japanese lycaenids is close to 61 (the status of some taxa is still a matter of debate — species or subspecies?), at least 44 %, but probably more than 50 % of the species are myrmecophilous.

There is again a distinct connection between faunal structure and myrmecophily. The 25 species of Japanese Polyommatini are probably all myrmecophilous, whereas in the Theclini myrmecophily is known only from three Arhopaliti species and one member of the Thecliti (*Shirozua jonasi*). The remaining 21 Thecliti species are apparently

secondarily myrmecoxenous, but due to their larval habits (most are living in the canopy of Fagaceae trees: Shirôzu 1962), ant-associations may have been partly overlooked.

The seven Eumaeini species contain few myrmecophiles (certainly documented for *Rapala arata* and *Satyrium w-album*, suspected for two further *Satyrium* species) and are thus similar to the Western Palaearctic Eumaeiti. The only representative of the Aphnaeini is obligatorily myrmecophilous as usual for this tribe, while the single members of the Miletinae, Curetinae and Lycaenini are all myrmecoxenous.

Overall, the majority of myrmecophilous lycaenids in Japan belongs to the tribe Polyommatini, whereas the lower proportion of myrmecophiles, when compared with the Western Palaearctic fauna, is due to the considerable diversity of one single largely myrmecoxenous subtribe, viz Thecliti.

Tab.11: Faunal composition and myrmecophily of Japanese Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	0	0	1	0	0
Curetinae	1	0	0	1	0	0
Lycaeninae	59	25	5/6?	59	34	5/6?
Aphnaeini	1	1	1	1	1	1
Lycaenini	1	0	0	1	0	0
Theclini	25	4	1	25	4	1
Eumaeini	7	2	0	7	4	0
Polyommatini	25	18	3/4?	25	25	3/4?
Lycaenidae	61	25	5/6?	61	34	5/6?

One must be aware that, for zoogeographical considerations, Japan is only a depauperate appendix of the Eastern Palaearctic. The lycaenid fauna of continental East Asia is much more diverse and, in particular, contains a larger number of species of myrmecophilous taxa like Polyommatiti or (towards the south) Arhopaliti.

Unfortunately, no comprehensive and taxonomically modern faunistic study of Chinese and East Siberian lycaenids is available, and the ecology of East Asian Lycaenidae is largely unknown. Hence, a detailed analysis of the Eastern Palaearctic is yet impossible, but most likely the proportion of myrmecophiles will turn out to be higher than in Japan, approaching the level of the Western Palaearctic (60—80 %).

Australia

Australia houses a lycaenid fauna of 133 known species, all of which belong to the subfamily Lycaeninae except a single representative of the Miletinae-Liphyrini. The ecology of Australian lycaenids is rather well known, the main source of data being the book of Common & Waterhouse (1981). Further information was derived from Grund & Sibatani (1975), Storey & Lambkin (1983), Atkins & Heinrich (1987), Hawkeswood (1987), Valentine & Johnson (1988), Samson (1989), Lambkin & Samson (1989), Braby (1990), and others.

Published information was found for 109 species, 74 of which (67.9 %) are myrmecophilous, including 28 obligately ant-associated species (25.7 %). The estimates for the entire fauna (133 species) yield about 120 myrmecophiles (90.2 %), including about 45 obligate ones (33.8 %).

These estimates are based on the assumption that only very few of the Theclini and Polyommatini (e.g. some *Philiris* species and the genus *Neolucia*) and a couple of Eumaeini (genus *Deudorix*) will finally turn out to be truly myrmecoxenous. For all other genera or species groups represented in Australia, close relatives are known to be ant-associated, lending support to the assumption that these groups as a whole are myrmecophilous.

The high proportion of obligate associations is still a rough estimate, since for a number of species in the genera *Hypochrysops, Jalmenus*, and *Ogyris* the obligateness of ant-associations requires further investigation. In any case, the Australian lycaenid fauna has both, a very high proportion of myrmecophiles in general (70—90 %) as well as a high percentage of obligate relationships to ants.

These figures are fairly close to the results of Pierce (1987) who gave a proportion of 72 % myrmecophilous lycaenids, including 35 % obligately ant-associated species. Some minor differences are due to more recently published information. However, my systematic estimate for the whole Australian fauna yields an even more extreme prevalence of myrmecophily, suggesting that, with very few exception, almost all Australian lycaenids are at least weakly ant-associated.

Again there is a significant systematic pattern. The Australian lycaenid fauna comprises two equally large tribes (Theclini and Polyommatini), while Deudorigiti and Liphyrini together contribute only 9 species. Within the Theclini, the endemic subtribes Luciiti, Ogyriti and Zesiiti are almost entirely myrmecophilous, as are the few members of the Oriental Arhopaliti in northern Australia.

Within the Polyommatini, the endemic Candaliditi and the *Theclinesthes* section of the Polyommatiti contribute most to the species diversity and are myrmecophilous with very few exceptions. The Eumaeiti contain a small number of myrmecoxenous species, but all typically myrmecoxenous systematic groups (Poritiinae, Curetinae, Lycaenini, Thecliti) are absent from Australia.

Australia is just a part of the Austro-Melanesian zoogeographical region southeast of Wallace's line. However, the present knowledge of the systematics and ecology of the

Tab.12: Faunal composition and myrmecophily of Australian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	1	1	1	1	1
Curetinae	-	-	-	-	-	-
Lycaeninae	108	73	27	132	119	≈43
Aphnaeini	-	-	-	-	-	-
Lycaenini	-	-	-	-	-	-
Theclini	50	44	24	62	58	≈40
Eumaeini	8	2	1	8	3	1
Polyommatini	50	27	2	62	58	2
Lycaenidae	109	74	28	133	120	≈45

Lycaenidae of New Guinea and its surrounding islands is too scanty to allow a more comprehensive analysis. There is some indication that the overall level of myrmecophily is somewhat lower in New Guinea.

Typically myrmecoxenous groups missing in Australia (Curetinae, Lycaenini) are at least weakly represented there, and the rather large genus *Philiris* (>60 species) appears to have a low level of myrmecophily (Forbes 1977, Parsons 1984, Wood 1984). Thus, the proportion of myrmecophiles in the entire Austro-Melanesian region may probably amount to 75—85 %.

Thailand and West Malaysia

The Lycaenidae fauna of the Oriental region is very rich in species with peak diversity in South East Asia ("Sundaland"). From the island Borneo alone 375 Lycaenidae species, i.e. more than three times the species diversity of Europe, are known (Seki et al. 1991). Thailand and West Malaysia are sufficiently well surveyed from the faunistic point of view (Corbet & Pendlebury 1978, Pinratana 1981) to allow at least a preliminary analysis of the distribution of myrmecophily, although ecological data are available only for a limited number of species.

The main aim of the inclusion of this area in the zoogeographical considerations is to provide data for one of the most species-rich parts of the world. Pierce (1987) only discussed India as part of the Oriental fauna, but this subcontinent has far less lycaenid species and its fauna is, to the north, strongly mixed with Palaearctic elements (e.g. in the Himalaya).

In total, approximately 450 Lycaenidae species occur in Peninsular Malaysia and Thailand with ecological information found for 119 species. Seventy-one of those (59.7 %) are known to be ant-associated including 7—14 (5.9—11.8 %) obligate myrmecophiles (this uncertainty is caused by the lack of sufficient new data).

Viewing at the whole fauna, an estimated maximum of 370 species (82.2 %) are myrmecophilous with probably less than 80 (17.8 %) obligatory cases. This estimate is based on the following assumptions.

All Poritiinae, Curetinae and Lycaenini are myrmecoxenous (this is true for all well documented Oriental members). In contrast, all Aphnaeini are myrmecophilous and probably even obligatorily so. Within the Miletinae, about 20 species are suspected to have a more than casual relationship towards ants, using ants as oviposition cues (like *Allotinus unicolor, Miletus* spp.) or even as larval food (probably less than 10 species of obligate myrmecophiles like *Liphyra brassolis, Allotinus apries?*). These high estimates are surely upper limits.

For the Theclini I have assumed that all Arhopaliti are myrmecophilous (as is true for all sufficiently well documented species), whereas the few Thecliti are supposedly myrmecoxenous, as are most of their temperate zone counterparts. I suppose that less than 50 Arhopaliti will finally turn out to be obligately myrmecophilous, but given the poor knowledge of that group this is a rather arbitrary figure.

In the Eumaeiti reductions of myrmecophily may be fairly common (only about one half of the Oriental species, for whom information is available, is surely ant-associated), and the assumption of less than 110 myrmecophilous species is certainly a very high upper limit. Within the Polyommatini most species are assumed to be myrmecophilous, but the figure of 10 obligate ant-associations is again almost certainly an overestimation (only one species, *Anthene emolus*, is yet certainly documented as being an obligate myrmecophile).

Thus, the true values for the proportion of myrmecophiles in general, and for obligate myrmecophiles among the lycaenid fauna of West Malaysia and Thailand, may well be lower than the above estimates (< 80 % and < 15 %, respectively).

Since the systematic structure has been used to construct these estimates, an analysis of systematic effects on the distribution of myrmecophily must be restricted to those cases with appropriate information available. An inspection of the data shows that the typical patterns are corroborated: a high proportion of myrmecophiles in the Aphnaeini, Theclini, and Polyommatini, with Eumaeini distinctly behind. Poritiinae, Curetinae, and Lycaenini are in fact myrmecoxenous, whereas the Miletinae contain a few specialized myrmecophiles.

This suggests that in South East Asia the proportion of myrmecophiles among the Lycaenidae fauna is rather high due to the preponderance of largely myrmecophilous taxa, but does not reach the extreme figures of Australia. The proportion of obligatorily myrmecophilous species, as well, is almost certainly distinctly lower than in Australia (10—20 %).

India

At present, a modern treatment of the Indian Lycaenidae is not available. For the purpose of this analysis I have thus compiled a preliminary species list using various sources (e.g. Bell 1915, Sevastopulo 1973, Pinratana 1981, Larsen 1987). This yielded a

Tab.13: Faunal composition and myrmecophily of Thai and West Malaysian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	1	0	0	27	0	0
Miletinae	14	7	2/4?	35	20 ?	10?
Curetinae	4	0	0	10	0	0
Lycaeninae	100	64	5/10?	378	<350	<70
Aphnaeini	2	2	2	7	7	7
Lycaenini	2	0	0	6	0	0
Theclini	14	11	1/4	132	130	<50?
Eumaeini	40	19	1	130	<110?	1?
Polyommatini	42	32	1/3?	103	<100	10?
Lycaenidae	119	71	7/14?	450	<370	<80?

minimum number of 247 species occurring in India, but due to the weak representation of the Himalaya region this is certainly an underestimate, the actual diversity being probably in the range of 300 species.

For 114 Indian lycaenid species ecological information was found with about 90 (78.9 %) being ant-associated, including 11—12 obligate myrmecophiles (ca. 10 %). Using these data and considering the taxonomic affinities, about 175—195 of the 247 recognized species are probably myrmecophilous (71—79 %) with some more than 20 (8.1 %) obligate myrmecophiles.

These estimates are again based on the assumption that Poritiinae, Curetinae, Lycaenini and Thecliti are myrmecoxenous, Aphnaeini and Arhopaliti are entirely myrmecophilous, and Polyommatinae are mostly myrmecophilous with few exceptions. The Eumaeini are considered to be largely myrmecophilous as well, but with a considerable number of myrmecoxenous species in the Deudorigiti, as suggested by the available evidence.

A comparison with the data of Pierce (1987) indicates some minor differences:

— First, Pierce based her study solely on the work of Bell (1915) and thus considered only 60 species.

— Secondly, the overall proportion of myrmecophiles is given with 75 %, which is practically identical to my results.

— Thirdly, she stated that 22 % of the Indian lycaenids investigated by Bell (i.e. 13 spp.) were obligate myrmecophiles. My data give a very similar absolute number of obligate myrmecophiles, but yield a distinctly lower percentage. This is most likely explained by the fact that obligate ant-associations are rather conspicuous in the field and have most strongly attracted the attention of the early lepidopterists, while myrmecoxenous species or rather weak ant-associations are underrepresented in Bell's work.

Thus, the overall pattern is that in India about 70—80 % of the Lycaenidae are ant-associated, but obligatory myrmecophily probably occurs in only about 10 % of the species.

The systematic faunal structure well explains this pattern. All known Aphnaeini larvae, and most Theclini and Polyommatini caterpillars are myrmecophilous, while about one fourth of the Eumaeini and all Curetinae, Poritiinae, and Lycaenini are myrmecoxenous. The myrmecophilous higher taxa clearly dominate the Indian fauna, but the myrmecoxenous taxa are sufficiently well represented to reduce the proportion of myrmecophiles to roughly the same level as in Europe or South East Asia.

Tab.14: Faunal composition and myrmecophily of Indian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	1	0	0
Miletinae	4	2	1/2	5	2	1/2
Curetinae	2	0	0	4	0	0
Lycaeninae	109	88/89	10	237	180/190	>18
Aphnaeini	3	3	3	9	9	9
Lycaenini	6	0	0	11	0	0
Theclini	15	13	3?	57	42	>3
Eumaeini	35	27	1	71	>53	1?
Polyommatini	50	45/46	3?	89	>77	5?
Lycaenidae	115	90/91	11/12	247	185/195	>20

South Africa

The South African lycaenid fauna (delimitations of the area considered following Pennington et al. 1978) is rather well known from both, systematics and ecology. According to Pennington et al. (1978) and updated with some more recent systematic treatments (e.g. Henning 1979, Henning & Henning 1984, 1989, Migdoll 1988, Bridges 1988), the lycaenid fauna of South Africa comprises about 341 species.

Life-history information is present for 208 species (main sources besides the above cited papers: Cottrell 1965, Clark & Dickson 1971, van Someren 1974, Sevastopulo 1975, Claassens & Dickson 1980, Henning 1983a, b, 1984a, b), with 104—109 ant-associated ones (50—52.4 %) including at least 55 obligate myrmecophiles (26.4 %). An extrapolation to the whole South African lycaenid fauna yields about 270 myrmecophilous species (79.2 %) including roughly 180 obligate myrmecophiles (52.8 %).

The reasoning for the latter estimates is as follows. The rather few Poritiinae and Lycaenini are suspected to be entirely myrmecoxenous, whereas the Aphnaeini are supposedly all myrmeco-

philous. Within the Polyommatini, the vast majority is myrmecophilous as well, with only few secondary reductions in the *Uranothauma* section. The Eumaeini probably contain a higher proportion of secondarily myrmecoxenous species (in the genera *Deudorix* and *Capys*, and possibly in *Iolaus*).

The South African Miletinae are, in contrast to their Oriental relatives, probably largely myrmecophilous, but this is due to the preponderance of one single genus, *Thestor*, which is subdivided in a number of local endemics in southern Africa and apparently has a close association with the ant genus *Acantholepis* (Clark & Dickson 1971, Claassens & Dickson 1980).

The extraordinarily high estimate for the proportion of obligate myrmecophiles in South Africa requires further explanation. The large number of presumed obligate myrmecophiles is due to only three systematic groups. One is the Miletinae genus *Thestor* with about 24 South African species.

The second group is the Polyommatini genus *Lepidochrysops* with about 55 South African species. Nearly all *Lepidochrysops*, whose life-history is sufficiently well known, live as parasites in *Camponotus* nests during the third and fourth larval instar (Cottrell 1965, 1984, Clark & Dickson 1971, Claassens 1976, Henning 1983a, b). It is strongly suspected that most *Lepidochrysops* species have a similar life-cycle.

The most diverse group of obligate myrmecophiles are the Aphnaeini with 124 recognized species in South Africa, and there is strong evidence that more than 70 % of this tribe are obligatorily associated with ants, mostly from the genus *Crematogaster*. Together, this results in the high estimate of more than 50 % of the South African lycaenids being obligatorily ant-associated. Henning (1987b) arrived at the same estimate.

A comparison with the figures of Pierce (1987) demonstrates significant differences. Pierce's evaluation was largely based on the works of Clark & Dickson (1971) and Claassens & Dickson (1980). The former exclusively covers species bred by the authors, while the latter is only concerned with a small subregion, the Table Mountain range.

Hence, Pierce (1987) considered only 107 species, 99 of which are myrmecophilous with a proportion of 27 % obligate myrmecophiles. This restricted range of species considered is the major reason for the differences between Pierce's analysis and the above one. The myrmecoxenous Poritiinae are distinctly under-represented in the books of Clark & Dickson (1971) and Claassens & Dickson (1980) and, accordingly, the overall proportion of myrmecophiles in the analysis of Pierce is probably too high.

In contrast, the species-rich genera *Thestor* (Miletinae), *Aloeides, Poecilmitis* (Aphnaeini), and *Lepidochrysops* (Polyommatini) are only partially treated in the above mentioned works, resulting in too a low estimate of the proportion of obligate myrmecophiles in the paper of Pierce (1987).

As has already pointed out above, the systematic faunal composition contributes importantly to the proportion of facultative and obligate myrmecophiles among the South African Lycaenidae. Two highly myrmecophilous taxa, Aphnaeini and Polyommatini, alone account for 70 % of the whole species diversity, supplemented by myrmecophilous members in the Miletinae and Eumaeini. The myrmecoxenous taxa Poritiinae and Lycaenini, in contrast, constitute less than 10 % of the lycaenid fauna.

In this respect, however, South Africa is not representative for the whole Ethiopian region. In tropical Africa, in particular, the Poritiinae-Liptenini form a significant compound (35 %) of the fauna. Supposing that at least half of them are truly myrmeco-

Tab.15: Faunal composition and myrmecophily of South African Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	14	0	0	30	0	0
Miletinae	12	4/9?	3/8?	27	≈ 24?	≈ 24?
Curetinae	-	-	-	-	-	-
Lycaeninae	182	100	>50	284	>245	>155
Aphnaeini	61	45	>35	124	124	>100
Lycaenini	2	0	0	2	0	0
Theclini	-	-	-	-	-	-
Eumaeini	35	9	0	43	>20	0
Polyommatini	84	46	>16	115	≈102	56
Lycaenidae	208	104/109?	>55	341	≈270	>180

xenous, and further considering that secondary myrmecoxeny does occur in a number of African Deudorigiti (e.g. *Capys*), Polyommatiti (*Uranothauma* section), and possibly Iolaiti, this reduces the overall proportion of myrmecophiles in the entire Ethiopian region to well below 80 %.

Likewise, the percentage of obligate myrmecophiles decreases. If, as a rough approximation, all *Thestor* and *Lepidochrysops* species, 80 % of the Aphnaeini, and 20 % of the Lycaenesthiti (*Anthene* and related genera) are considered to be obligatorily associated with ants, this results in an absolute number of approximately 400 species (less than 30 % of the roughly 1500 Ethiopian lycaenids). For a more detailed and comprehensive analysis, more data from the tropical areas of Africa are clearly needed.

Neotropical region

The Neotropical lycaenid fauna is very rich in species (>1000), but only two higher taxa are represented: Eumaeiti (the vast majority) and Polyommatiti (far less than 50 spp.). Ecological data are very scant, and the taxonomy and faunistics are still in a premature state. Mainly from these reasons Pierce (1987) decided not to include the Neotropics into her analysis. I here give a very preliminary view which, nevertheless, should allow to estimate upper and lower limits for the proportion of myrmecophiles among the Neotropical lycaenids.

Life-history information is available for roughly 160 species occurring south of the United States (Tab.17 and Robbins, pers. comm.). More than 150 of the species covered belong to the Eumaeiti. The few Neotropical Polyommatini are poorly documented,

but several species of *Hemiargus*, *Brephidium* and *Zizula* are known to be myrmecophilous. The ecology of the Andine representatives of the *Hemiargus* group (Nabokov 1945) is unknown.

Ant-associations have been recorded for only 17 Neotropical Eumaeiti species (12.2 %), and no single case of myrmecophily among Neotropical Lycaenidae has yet surely been established as being obligatory. In contrast, 27 species (17.3 %) have been explicitly stated to have no ant-associations.

Assuming that closely related species (belonging to the same genus) have similar degrees of myrmecophily, the presumed percentage of myrmecophilous species increases to 27.6 %, while the proportion of myrmecoxenous Eumaeiti becomes 26.3 %. Notwithstanding the meagre database, the following conclusions can be drawn:

— First, myrmecophily is clearly less widespread and less strongly developed among the Eumaeiti than in other large lycaenid subtribes. Otherwise more ant-associations would have been reported, as it is the case for the tropical regions of Africa and Asia. The limited number of well documented myrmecophiles among the temperate zone Eumaeiti further corroborates this conclusion.

— Secondly, obligate myrmecophily is rare within the Eumaeiti, if it does occur at all. Obligate associations are more likely to be detected than facultative ones, especially in such species where larvae or pupae regularly occur inside ant nests. No such case is hitherto known from Neotropical lycaenids (but from Riodinidae: Harvey 1987, Ballmer, pers. comm.).

— Thirdly, reductions of myrmecophily have occurred several times in parallel. Examples are the genera *Eumaeus, Arcas, Contrafacia*, and *Erora*, where even the DNO is virtually absent.

Overall, the Neotropical lycaenid fauna appears to be characterized by a rather low proportion of myrmecophiles. Furthermore, many species presumably have only loose, facultative ant-associations, and obligate myrmecophily is surprisingly rare.

Nearctic region

North America's lycaenid fauna is taxonomically well known. Nevertheless, our knowledge of its ecology and larval myrmecophily is still incomplete. The majority of recorded ant-associations dates from the last decade (e.g. Harvey & Webb 1980, Ballmer & Pratt 1988, and in press, Harvey & Longino 1989). Therefore, further additions may well occur, in particular from species with arboricolous larvae where the available life-history information is largely based on oviposition records and subsequent laboratory rearings.

For 111 of the 112 resident lycaenid species of North America (species concepts following Scott 1986 and Ballmer & Pratt 1988, Riodinidae excluded) life-history information is available. Only 33 species (29.7 %) have been reported being ant-associated, 23 of those belonging to the Polyommatini, whereas only six Eumaeiti and four Lycaenini species are surely known to be myrmecophilous.

No Nearctic lycaenid is yet known to be obligatorily myrmecophilous, but since recent work on Swiss populations of the Holarctic Polyommatine *Plebejus idas* indicates that this species may have an obligate relationship to certain *Formica* ants (Jutzeler 1989d), it is well possible that North American populations do so as well.

An estimate for the whole Nearctic fauna yields at least 45 myrmecophilous species (40.2 %). It is very likely that all Polyommatini species, except the myrmecoxenous arctic or alpine genera *Agriades* and *Vacciniina*, are at least facultatively associated with ants. In addition, at least another four Eumaeiti species are supposed to be myrmecophilous, judging from their close relatives, but in the course of a more thorough knowledge of the ecology of Eumaeiti larvae in the field, this number may well increase further.

When comparing these figures with the data given by Pierce (1987), one has first to consider that in this latter paper the riodinids were treated as a lycaenid subfamily. Removing them, the 23 cases of ant-associations cited by Pierce give a 20.5 % proportion of myrmecophiles (total of 112 species). The differences to the analysis presented above are mainly due to the recent additions to the list of North American myrmecophiles by Ballmer & Pratt (1988, and in press) and Harvey & Longino (1989). When the systematic relatedness is taken into acount, this well doubles the percentage given by Pierce (1987).

As in all other zoogeographical regions considered here, the systematic structure of the Nearctic lycaenid fauna closely parallels the distribution of myrmecophily. Ant-associations are unknown from the Miletinae and Thecliti (only 3 species altogether), but are abundant among the Polyommatini. Only 10 % of the Nearctic resident Eumaeiti have hitherto been reported being myrmecophilous, and 4 of 15 Lycaenini species have evolved an interesting alternative pathway towards myrmecophily.

The predominance of one subtribe with a pronounced tendency to reduce ant-associations (the Eumaeiti contribute 53.6 % to the species diversity) is responsible for the rather low overall proportion of myrmecophiles among the North American Lycaenidae.

Tab.16: Faunal composition and myrmecophily of North American Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	0	0	1	0	0
Curetinae	-	-	-	-	-	-
Lycaeninae	110	33	1?	111	≈45	1?
Aphnaeini	-	-	-	-	-	-
Lycaenini	15	4	0	15	4	0
Theclini	2	0	0	2	7	0
Eumaeini	60	6	0	60	≈10	0
Polyommatini	33	23	1?	34	31	1?
Lycaenidae	111	33	1?	112	≈45	1?

Conclusions

1.) In contrast to the opinion of Pierce (1987), most higher taxa of the Lycaenidae show peculiar and characteristic distributions. These distributions correspond well to the continental plates, or subregions of those: Liptenini, Liphyrini, Aphnaeini and Lycaenesthiti are centred in Africa; Luciiti, Zesiiti, and Candaliditi in Austro-Melanesia; Poritiini, Miletini, Curetinae, Arhopaliti, Catapaecilmatiti, Loxuriti, Remelaniti, and Niphanditi in southern Asia; Thecliti in East Asia; and Eumaeiti in the Neotropics.

Most of these tribes or subtribes are even restricted to the above mentioned regions, while others weakly extend into adjacent realms. As a consequence, these distributional patterns result in characteristic and very different systematic compositions of the lycaenid faunas of all regions investigated.

Although the detailed phylogenetic relationships between the higher lycaenid taxa are not yet clear, the observed patterns strongly point towards historical and evolutionary processes associated with plate tectonics. Obviously, the evolution of the higher lycaenid taxa is strongly correlated with the break-up of the Mesozoic south continent Gondwana. This connection of the Lycaenidae to Gondwana was already noted by Pierce (1987).

The north continent Laurasia probably had no lycaenid fauna when it separated from Gondwana, and since North America split off early from the remainder of the north continent ("proto-Eurasia"), it became isolated for a long period and was only late colonized by lycaenid stocks from South America (Eumaeiti) or Asia (Polyommatiti). Only the Nearctic Miletinae *Feniseca tarquinius* may have entered North America from Europe via the Thule bridge during the Tertiary.

The eastern part of the north continent ("proto-Eurasia"), as well, seems to have been only secondarily colonized by lineages from the south (via the Iberian bridge in the southwest and via Sundaland in the southeast: Eliot, pers. comm.), indicating that the primary evolution of higher lycaenid taxa took place in Gondwana and its subsequent fragments.

The details of this story remain to be uncovered. In particular, the role of India and Australia are a matter of debate: Do the Australian endemics (Luciiti, Ogyriti, Candaliditi) represent an ancient stock, or did they colonize Australia secondarily? Did India carry any significant lycaenid fauna from Africa towards Asia?

In any case, one major event in the break-up sequence of Gondwana, the separation of South America from Africa, has a close parallel in the distribution of lycaenids: the African and Oriental Deudorigiti and their Neotropical sister-group Eumaeiti.

2.) The characteristic distributional patterns of higher lycaenid taxa, and the resulting different faunal structures due to the subsequent radiation of these taxa, have a significant corollary with respect to myrmecophily. Regions where taxa with a low level of myrmecophily predominate (Thecliti in eastern Asia, Eumaeiti in the Americas), must necessarily have a lower proportion of myrmecophiles than regions with a preponderance of highly myrmecophilous groups (e.g. Aphnaeini and Polyommatini in Africa, Polyommatini in Europe, Polyommatini and Theclini in Australia).

Thus, again contradicting the work of Pierce (1987), the evolutionary histories and faunal compositions of the different zoogeographic regions do explain, to a considerable degree, the observed geographical patterns of myrmecophily.

3.) The clear-cut north-south disparity in the proportion of myrmecophily claimed by Pierce (1987) could not be confirmed. Instead, in most areas of the Old World, including the Western Palaearctic (Fiedler 1991), the proportion of myrmecophiles is 70—80 %. A higher value may occur in Australia with its depauperate and specialized fauna, and lower percentages occur in Japan (a depauperate part of the Eastern Palaearctic) and in the New World. All these deviations are easily explained by the respective faunal compositions, i.e. by their colonization history. Two examples may illustrate this.

North America, with its low proportion of myrmecophiles, was mainly colonized by three lineages. The myrmecoxenous Lycaenini and the myrmecophilous Polyommatini arrived from the Palaearctic through a northern route. Climatic constraints possibly limited a more extensive invasion, but both taxa largely retained their characteristic relationships to ants. A few Polyommatini (*Leptotes, Zizula, Brephidium*) are supposed to have arrived via wind dispersal across the Atlantic ocean, and these as well have retained the myrmecophily of their African relatives.

The Eumaeiti invaded from the Neotropics without changing much their already low level of myrmecophily. This southern route allowed a more extensive invasion, resulting in the preponderance of Eumaeiti in the today North American lycaenid fauna.

Thus, there is no reason to assume that ecological (abiotic or biotic) factors primarily caused the rather low proportion of myrmecophily in the Nearctic, although the climate may well have secondarily shaped the level of ant-associations (reductions of myrmecophily appear to be favoured in arctic or alpine tundra habitats, in boreal forests, or in the canopy of temperate zone Fagaceae forests; see above).

The Western Palaearctic, with its high proportion of myrmecophiles, has a completely different history. Although the majority of the lycaenid fauna was certainly exterminated during the glaciations, refugial areas existed in the Mediterranean area and in non-glaciated regions of Asia. As a consequence, a rapid recolonization was possible, allowing a rather rich fauna of largely myrmecophilous Polyommatini to invade into Europe again.

Other tribes only survived or recolonized in limited numbers, whereas the tropical subfamilies Poritiinae, Miletinae, and Curetinae did not manage to cross the geographical barriers (North African and Arabian deserts, Western and South Central Asian mountain ranges). Again climatic factors have secondarily shaped the level of myrmecophily, e.g in high latitudes.

4.) The north-south disparity in the obligateness of myrmecophilous associations remains to be further investigated. In the Palaearctic, only about 10 % of the lycaenids are obligatorily myrmecophilous. A similar estimate was attained for India. In South East Asia, the obligate myrmecophiles most likely constitute less than 20 % (and possibly less than 15 %) of the entire lycaenid fauna.

In contrast, South Africa (27 %) and Australia (35 %) have very high percentages of obligate myrmecophiles, whereas among the New World lycaenid fauna, although less well understood, such associations appear to play almost no role.

These data indicate that, instead of a clear-cut disparity, a gradient in the proportion of obligatory ant-associations is likely to exist. The highest percentages occur in South Africa and Australia, the lowest in the Palaearctic, with the more tropical regions of India, South East Asia, or New Guinea apparently being intermediate.

Whatever the exact figures may be, distinct differences in the obligateness of ant-associations between several zoogeographical regions seem to be real. The question as to what evolutionary processes have led to this pattern will be discussed, among others, in the final chapter.

EVOLUTION OF INTERACTIONS BETWEEN LYCAENIDS AND ANTS

Ants as selective agents for lepidopterous caterpillars

The leading role of ants as predators of arthropods (e.g. Hölldobler & Wilson 1990) has often been demonstrated. Rather slowly moving and weakly sclerotized organisms like most Lepidoptera caterpillars, in particular, provide nearly prototypical ant prey.

As a consequence, predatory ants are important regulators of caterpillar abundance (e.g. the ant genus *Formica*: Laine & Niemelä 1980, Gösswald 1989) that significantly influence the overall level of herbivory (Warrington & Whittaker 1985) or may even shape the guild structure of phytophagous caterpillars (Ito & Higashi 1991).

The influence of ants on caterpillar survival may differ between larval instars or between various ant species (Tilman 1978, Weseloh 1989), and it may further interfere with the caterpillars' parasitism rate (Jones 1987). Clearly, ant predation is a weighty selective pressure for Lepidoptera larvae, and a number of life-history traits and adaptations of the latter may be seen, at least in part, as a defensive response towards ants.

Bernays & Cornelius (1989) observed that the ant *Iridomyrmex humilis* preferentially preyed upon polyphagous caterpillars, suggesting that food specialists (especially monophagous species) are typically more effective in the extraction and storage of toxic plant chemicals which help to deter predators (see also Bernays 1988).

Further support for this hypothesis comes from the studies of Bernays & Montllor (1989) and Bowers & Larin (1989) who observed that aposematic caterpillars feeding on toxic plants (*Uresiphita reversalis* [Pyralidae] and *Eumaeus atala* [Lycaenidae]) were rejected by ants as prey. However, the aposematic caterpillars of the arctiid moth *Tyria jacobaeae*, although sequestering considerable amounts of pyrrolizidine alkaloids, are heavily preyed upon by ants (Myers & Campbell 1976, Vrieling et al. 1991).

Generally, the use of plant semiochemicals is extremely widely distributed among the Lepidoptera as defensive device (for a review see Brower 1984), and it should be noted that the majority of Lycaenidae caterpillars are food specialists (see above) whose hostplants contain toxic secondary compounds (cyanogenic glycosides, alkaloids, and others).

A more elaborated way of chemical defence, when disturbed, is the regurgitation of foregut contents with toxic plant semiochemicals (Common & Bellas 1977, Eisner et al. 1980, Brower 1984, Leather & Brotherton 1987, Peterson et al. 1987), or the release of defensive secretions from specialized exocrine glands (e.g. Eisner et al. 1970, 1972, Honda 1983a, b, Witthohn & Naumann 1987).

In the examples mentioned here these defensive devices have been shown to be effective against ants. Numerous lycaenid larvae also regurgitate when disturbed (e.g. *Polyommatus coridon*: Fiedler, unpublished), and since the latter species feeds on cyanogenic hostplants (*Hippocrepis, Coronilla*) its regurgitations may provide a powerful defense.

Numerous other protective adaptations have evolved among the Lepidoptera. Many caterpillars are hairy (e.g. Lasiocampidae, Arctiidae, Lymantriidae), and this provides

some protection against ant attacks at least in later larval instars (Ayre & Hitchon 1968, Tilman 1978). Other caterpillars escape by dislodging on silk threads (e.g. Leather & Brotherton 1987), but this strategy is not invariably effective against ants (Allen et al. 1970). Further defensive behavioural responses to predatory attacks are dropping off from the hostplant, thrashing against potential enemies and others (Cornell et al. 1987), and all these may be involved in the defence against ants.

A very important protective life-history trait is endophytism. Endophytic larvae (those boring in stems or living in shelters of leaves spun together) are readily attacked and killed when deprived of their protective envelope (Bernays & Cornelius 1989), but in the field such larvae easily survive even in habitats densely populated with ants (Allen et al. 1970, Ito & Higashi 1991). Notably, numerous lycaenid caterpillars (especially in the Deudorigiti and Eumaeiti, see above) are endophytic.

These examples may suffice to demonstrate that ant predation is an important selective agent in the evolution of Lepidoptera caterpillars and that a number of defensive or protective mechanisms are realized within this large taxon of herbivorous insects.

Nevertheless, the ants must be viewed differentially as well. Whereas some ant subfamilies are entirely or predominantly predatory (Ponerinae, Ecitoninae, Dorylinae), others contain a large proportion of trophobiotic species (Pseudomyrmecinae, Myrmicinae, Dolichoderinae, Formicinae). Indeed, the trophobiotic ant subfamilies contribute most to the species diversity of the family Formicidae.

Furthermore, the level of ant predation shows a marked latitudinal gradient (Jeanne 1979) with the highest predatory pressure arising from ants in the tropics.

Thus, the complex of adaptations that allows caterpillars to avoid the attacks of trophobiotic ants — and only these are involved in myrmecophily of butterfly caterpillars (DeVries 1991, this study) — yields an enormous twofold selective advantage. A large number of ant species is excluded from the potential enemy guild, and this coexistence with ants enables these caterpillars to colonize ecological niches with a high abundance of ants, but distinctly fewer competitors and enemies ("enemy-free space": Atsatt 1981a).

As has already been emphasized by Lenz (1917) and Malicky (1969b, 1970a), this was certainly the leading selective advantage at the beginning of the evolution of lycaenid myrmecophily (see also DeVries 1991).

Evolution of myrmecophily and its related organs

As has been discussed in the systematic chapter in detail, myrmecophily must be viewed as an apomorphic strategy within the Papilionoidea, where it is confined to, and has independently evolved in, distinct groups of the families Riodinidae and Lycaenidae. In both families myrmecophily is highly correlated with the presence of specialized secretory ant-organs (Cottrell 1984, DeVries 1988, 1991, this study), and the extant primarily myrmecoxenous subfamilies lack such organs (Hamearinae in the Riodinidae; Poritiinae and Miletinae in the Lycaenidae: Harvey 1987, this study). Thus,

the caterpillars of these groups may serve as models for the ancestors of the myrmecophilous taxa. In this chapter I will discuss some ideas on the phylogeny of the Lycaenidae in connection with the evolution of their ant-organs and ant-associations.

Within the Riodinidae, the classification of Harvey (1987) suggests a convincing parallelism between the evolution of ant-organs and myrmecophily. The caterpillars of primitive subfamilies (Hamearinae, Euselasiinae) and of several Riodininae tribes (Riodinini, Symmachiini, Stalachitini etc.) are hairy, lack ant-organs, and are never associated with ants.

In the less advanced myrmecophilous tribe Eurybiini (and possibly in Mesosemiini, but available records need confirmation), a pair of tentacle nectary organs evolved, whose function is analogous to the DNO of lycaenid caterpillars. Eurybiini (with only 23 recognized species) have facultative and unspecific ant-associations.

In the two most advanced tribes, the sister-groups Lemoniini (about 70 species) and Nymphidiini (190 species), two further types of ant-organs are present: the anterior tentacle organs (with a function apparently analogous to the TOs of lycaenid larvae, i.e. activating and alerting attendant ants), and a pair of vibratory papillae that produce vibrational signals to communicate with ants (Cottrell 1984, DeVries 1988, 1990a).

Some Nymphidiini larvae bear a fourth type of organs possibly related to myrmecophily ("bladder setae"), and these species apparently maintain obligatory relationships to ants (*Azteca, Crematogaster*: Harvey 1987, DeVries, pers. comm.).

Thus, there is a parallel increase in the number of ant-organs present, complexity and prevalence of ant-associations, and species diversity from Eurybiini towards Lemoniini and Nymphidiini. In short, the evolution of riodinid myrmecophily can be summarized by the sequence: protective devices (hairiness: coexistence) — trophobiotic glands (tentacle nectary organs: loose facultative mutualism) — communicative organs (anterior tentacle organs, vibratory papillae: stable mutualisms) — specific secretory organs ("bladder setae": obligate mutualisms).

The evolutionary sequence within the Lycaenidae is less clear. Since the hypothesis of ancestral myrmecophily (Pierce 1987, Scott & Wright 1990) had to be rejected by evidence from a systematic comparison (this study), myrmecophilous organs are supposed to have been absent in the caterpillars of ancestral Lycaenidae. A reasonable assumption is that ancestral lycaenid caterpillars resembled the larvae of extant Poritiinae or, possibly, Hamearinae.

If this is true, then the ancestral lycaenid larvae can tentatively be reconstructed as rather small, slowly moving, moderately hairy insects, which most likely already possessed lenticle-like setae. Modern Poritiinae effectively coexist with ants based on these "passive" preadaptations. It is yet unknown whether or not the typical leathery cuticle of higher lycaenids belonged to the groundplan of lycaenid caterpillars, as well.

The ability to completely retract the head under the prothoracic shield is well developed only in some Miletinae and the Lycaeninae tribes Lycaenini, Theclini, Eumaeini and Polyommatini, whereas Curetinae and Aphnaeini larvae lack this character. Therefore, this significant adaptation is very likely not a groundplan character of the Lycaenidae,

but has convergently evolved in two taxa whose larvae regularly interact with ants (homopterophagous Miletinae, myrmecophilous Lycaeninae).

Two plant taxa are candidates for being the primary lycaenid hostplants: Fabales (as modern Curetinae) or, perhaps less likely, Fagales (as *Poritia erycinoides*).

Probably, the larvae of ancestral lycaenids were primarily not truly attractive to ants. From behavioural observations there is no indication that the lenticles or pore cupola organs of Poritiinae, Miletinae, Curetinae, or Riodinidae produce secretions attractive to ants (see above). The tight connection of the PCOs to myrmecophily seems to be an apomorphic, secondary trait of the subfamily Lycaeninae, and these organs probably changed their function at least once during lycaenid phylogeny. It cannot be ruled out, however, that the ancestral PCOs could have played a role in mediating "ignorance" or "appeasement", but the chemical basis of these preadaptations for myrmecophily is not yet understood (DeVries 1991).

At any rate, the hypothetical ancestral lycaenid caterpillars were able to colonize habitats abundantly populated with ants. Such microhabitats are plants bearing extrafloral nectaries, plants colonized with trophobiotic Homoptera, or plants supporting ant nests. This is evidently a considerable selective advantage, since "normal" herbivorous caterpillars require special and often rather costly defensive adaptations to survive in such habitats. Three major lycaenid lineages have radiated starting from this primary myrmecoxeny.

The Poritiinae are the most diverse group of these. One of their tribes, the Oriental Poritiini, remained phytophagous, but nothing is known on their interactions with ants. The African tribe Liptenini tremendously diversified (today 520 species) in a very unusual nutritional niche: they specialized upon lichens. Liptenini larvae are known to coexist with ants where the latter are very abundant, and some species are presumed to maintain even commensalic relationships to the ant genus *Crematogaster.*

Since feeding on lichens and on detritus require similar specializations of ingestion and metabolism (Rawlins 1984), lichenivorous insects are possible candidates for the evolution of scavenging or refuse-feeding life-habits in ant nests (see also Ayre 1958).

Thus, Poritiinae larvae demonstrate the evolutionary effectiveness of coexistence with ants, but their greatest diversity probably evolved in relation to an unusual host shift. Overall, Poritiinae larvae never evolved specialized ant-organs and their interactions with ants are mostly governed by protective adaptations.

The subfamily Miletinae made a significant shift in larval nutrition towards aphytophagy. Atsatt (1981a) and Cottrell (1984) have discussed possible pathways leading to these highly untypical feeding habits. They assume that Miletinae carnivory started from ancestors feeding on fruits and other protein-rich plant parts. Given the presumed sister-group relation between Poritiinae and Miletinae, however, the ability to metabolize chitinous fungal components of lichens could as well represent a phyletic predisposition for carnivory. Only a better resolved phylogeny can help to decide between these alternatives.

Irrespective of this, Miletinae caterpillars as predators of Homoptera were regularly confronted with aggressive ants that defend their honeydew sources. Accordingly, Miletinae larvae were only able to exploit this food resource on the grounds of protective adaptations against ant-attacks. In fact, ants usually ignore highly adapted Miletinae caterpillars (*Miletus, Allotinus, Logania, Megalopalpus, Aslauga*), while less advanced genera (*Feniseca, Taraka, Spalgis*) additionally construct protective silken shelters wherein the larvae live, or they cover themselves with remains of their prey.

There is no evidence that Miletinae larvae in general secrete substances attractive to ants, their PCOs eliciting little interest in the ants attending homopterans. Some specialized taxa, however, became true myrmecophiles, pupating in ant nests (*Miletus*: the pupae posess glands highly attractive to ants; Roepke 1919), feeding inside ant nests on grubs (*Liphyra, Thestor?, Allotinus apries?*), or even eliciting trophallactic regurgitations (*Euliphyra*). These latter myrmecophiles are attractive to their host ants, possibly imitating their specific brood odour. Only *Liphyra* is regularly attacked, but resists ant-attacks due to its protective carapax-like cuticle (Cottrell 1987).

In all, the Miletinae represent a rather small taxon with amazing specializations, but its evolution is mainly based upon coexistence with ants, true myrmecophily having arisen several times independently from the carnivorous life-habits and the close association with trophobiotic ant-tended homopterans.

The third subfamily representing primary myrmecoxeny are the Curetinae. Their larvae feed on young foliage of Fabales where usually ants forage at extrafloral nectaries (DeVries 1984, Maschwitz & Fiedler, unpublished). Ants do neither attack the caterpillars, nor do they form close, stable associations with the latter. The peculiar TOs of *Curetis* larvae are defensive organs and are everted upon disturbance. No relation of the TOs or of the further specialized epidermal organs (DeVries et al. 1986) to myrmecophily is yet apparent.

In summary, larvae of the lycaenid subfamilies Poritiinae, Miletinae and Curetinae occupy ecological niches where the avoidance of ant-attacks is advantageous (plants with extrafloral nectaries) or even necessary (trophobiotic associations). Furthermore, their larvae possess a number of specialized epidermal organs, including TOs in two small subgroups, but none of these are hitherto known to be involved in interactions with ants.

The diversity of these three subfamilies is rather poor, representing less than 17 % of the described lycaenid species worldwide. Only one lineage (Liptenini) has diversified considerably in a distinct adaptive zone, viz. the shift towards lichenophagy.

With few secondary exceptions, the larvae of the primarily myrmecoxenous subfamilies were unable to achieve benefits beyond the enemy-free space from their "associations" with ants. Only Lipteniti caterpillars on trees infested with *Crematogaster* ants, or Miletinae larvae in trophobiotic associations or ant nests, probably enjoy some reduction of the pressure exerted by parasitoids or predators. Thorough ecological or behavioural investigations on these taxa are needed.

The most advanced subfamily Lycaeninae has transcended this spectrum of relationships with ants and has entered into mutualistic trophobiotic associations with ants. Unfortunately, the detailed historical sequence of the adaptive steps that have led to this true myrmecophily cannot yet be unravelled.

At the very beginning, myrmecoxenous larvae may have responded to ant-attacks with the exudation of small amounts of hemolymph or the production of frass pellets (compare the forced defaecation of aphids [*"Angstkoten"*] when attacked; or the anal exudates of the tortricid genus *Semutophila*: Maschwitz et al. 1986). Fresh moist caterpillar frass can be attractive to ants as it contains amino acids and possibly other nutritive plant compounds. I have repeatedly observed that lycaenid larvae (including myrmecophilous species) respond to occasional ant-attacks with defaecation (this study).

Certainly, the integration of the PCOs into the functional complex of ant-associations was an important early step in the evolution of Lycaeninae myrmecophily. PCOs and some further glandular setae suffice to induce stable ant-associations in some North American *Lycaena* species (Ballmer & Pratt 1988), and such associations possibly yield protective benefits to the caterpillars, although the ants receive only marginal rewards.

However, ant-associations of most *Lycaena* caterpillars and of other species without a functional DNO are fairly unstable even in the laboratory (this study), and they rarely occur in the field. Thus, the evolution of the DNO and its related nutritive secretions, as a keystone synapomorphy of the Lycaeninae, was obviously the decisive step towards myrmecophily. DNO secretions considerably improve the stability of ant-associations.

The histological investigations of Malicky (1969b) suggest that the DNO might have originated from glandular hairs, while Kitching & Luke (1985) imply that the DNO might be derived from secretory epidermal pores. A phylogenetic connection between the DNO and the abdominal glands of lymantriid caterpillars (Shields 1989b) lacks any supporting evidence and was already refuted by Malicky (1969b).

The evolutionary history of the TOs is less clear. The potential to evolve eversible structures must have been widespread in the Riodinidae and Lycaenidae. Two types of TOs in the Riodinidae are closely connected with myrmecophily, but among the Lycaenidae a relation of the TOs to ant-association is only known from the Aphnaeini and the higher Lycaeninae tribes, whereas the respective eversible organs of Curetinae and *Aslauga* (Miletinae) probably evolved independently in a different functional context (defence?).

The evolution of ant-related TOs in the Lycaeninae possibly started with glandular scent hairs. One can speculate that the volatile secretions of such hairs could be used more efficiently and economically, if the hairs are only extruded when required. Accordingly, cuticular sheaths and a mechanism for eversion and retraction were developed, leading to the complex TOs of extant lycaenids.

Malicky (1969b) suggested that DNO and TOs first evolved as metameric organs, that were later reduced on most body segments and were retained only in special locations. This hypothesis was mainly founded on the different locations of TO-like structures in

Riodinidae and Lycaenidae caterpillars, and on the presence of additional secretory structures ("dish organs") on some abdominal segments of certain Aphnaeini larvae. However, since recent systematic and morphological work strongly indicates that myrmecophily and its related organs evolved independently in both families (e.g. DeVries 1990b, this study), the assumption of a multisegmental groundplan of ant-organs has to be rejected.

Given the very sporadic occurrence even among the Aphnaeini, the "dish organs" of *Spindasis* or *Crudaria* are peculiar apomorphic structures of these genera rather than being rudiments of ancestral nectary organs on additional abdominal segments. The apparent restriction of eversible glandular structures like the DNO and TOs to the fore or rear end of riodinid and lycaenid larvae may be due to interferences of the function of such organs with caterpillar locomotion.

Once the myrmecophilous organs had been developed, the enhancement of ant-associations via additional nutritive rewards (DNO) and communicative signals (TOs, vibrational communication?) must have resulted in a significant positive feed-back (higher rate of larval survival), and evidently this process reinforced the rapid evolution and radiation of larvae with a complete set of myrmecophilous organs.

The Aphnaeini, as the presumed first group that has split off from the Lycaeninae stem (Eliot 1973, and pers. comm.), even possess the most complex ant-organs (highly specialized TOs, "dish organs"). In this respect, the Aphnaeini might be viewed as an early "experimental" stage of lycaenid evolution, whereas later on the equipment with ant-organs, their morphology and function remained surprisingly constant. In fact, except the numerous reductions of myrmecophilous organs (see below) and the great diversity of secondary setae, the roughly 3300 species of the tribes Theclini, Eumaeini, and Polyommatini present a nearly monotonous view with regard to their ant-organs.

In short, the evolution of lycaenid myrmecophily may be simplified as follows:

1) only "passive" protective characters present (small, onisciform, moderately hairy, slowly moving caterpillars, PCOs present): coexistence with ants;
2) ant-attractive secretory organs evolve (PCOs become integrated into myrmecophily, trophobiotic DNO evolves): mutualism;
3) specific communicative signals evolve (chemical specialization of PCO and DNO secretions, pheromone mimics?): obligate mutualism or parasitism; or
4) trophobiotic glands become reduced: secondary myrmecoxeny.

In this scenario, a few myrmecophiles (Liptenini, Miletinae) have independently evolved from stage 1. The "typical" myrmecophily of lycaenid larvae is represented by stage 2, with alternatives 3 and 4 being optional. TOs may have evolved at stage 1 having later been integrated into communication with ants, or they could have evolved independently at stage 2.

This hypothesis reverses the view of Malicky (1969b) that multisegmental DNOs and TOs preceded the evolution of PCOs, and that the most advanced lycaenids rely on PCOs alone with respect to myrmecophily. However, the comparative evidence from Riodinidae and Lycaenidae morphology renders Malicky's view unlikely.

A more complete picture of the evolutionary sequence that has led from myrmecoxenous lycaenids only exhibiting passive protective characters to the Lycaeninae with their sophisticated mutualistic or parasitic ant-associations will only arise on the grounds of a more detailed knowledge of the interactions between more ancestral lycaenid caterpillars and ants, the morphology and histology of their epidermal organs, and the chemical composition of the secretions of PCOs and other setae. Overall, a more thorough phylogenetic approach is highly desired.

Specializations and reductions

Obligatory myrmecophily

While the primary steps in the evolution of lycaenid myrmecophily could only roughly be outlined above, the specializations and reductions that have further occurred can be discussed in greater detail on the grounds of available comparative data.

The ant-associations of ancestral Lycaeninae were most likely unspecific and facultative, as are the ant-relationships of most extant Lycaenidae, Riodinidae, as well as of most trophobiotic Homoptera. However, obligatory and specific ant-associations do occur in a number of lycaenid caterpillars, and the question arises as to when and how specific ant-associations have evolved in the Lycaenidae.

First, what selective advantages may accrue to an obligate and specific myrmecophile? Obligate myrmecophiles are able to enter into ant nests or may even be actively adopted. Living in ant nests surely provides the most pronounced protection against other larval enemies, although highly specialized parasitoid ichneumonids even manage to parasitize *Maculinea* caterpillars inside *Myrmica* nests (Thomas, pers. comm.).

In addition, larvae living in ant nests may utilize ant brood as food resource. However, since ants are most aggressive against intruders in and near their nests, myrmecophiles will only be tolerated there if they are either well integrated into their host colony (using appropriate signals), or if they possess effective protective devices against fatal attacks.

The majority of obligatorily myrmecophilous Lycaenidae in fact lives in ant nests at least during one stage of their development. Numerous Aphnaeini, Theclini and Polyommatini pupate, rest or diapause in ant nests, and host-specificity appears to be distinctly beneficial in these cases. Similarly, all species where the larvae feed on ant brood (e.g. *Liphyra, Acrodipsas, Maculinea, Lepidochrysops*) or receive ant-regurgitations (*Euliphyra, Spindasis, Shirozua, Maculinea*), maintain genus-specific relationships to ants at least, and most of them are suspected to use specific communication signals. So, inquilinism strongly selects for host-specificity in myrmecophilous lycaenids.

A second possible benefit from specific ant-associations is a low risk of "accidental mortality". Generalized signals cannot be optimal for all ant species a larva potentially encounters. Accordingly, some caterpillars might be killed by ants despite their myrmecophilous adaptations, and anecdotal evidence as well as some experimental data (Malicky 1961, 1970b) suggest that such accidental mortality does occur.

This ecological risk is most pronounced with dominant and aggressive ant species, and this might select for specializations of the larval signals. Optimized communication between a lycaenid species and its ant partner, then, could yield an improved protection against enemies.

This hypothesis is supported by the experimental data of Pierce & Eastseal (1986) and Pierce et al. (1987): the protective benefits from ant-association in the obligate myrmecophile *Jalmenus evagoras* by far exceeded those in the facultative myrmecophile *Glaucopsyche lygdamus*. Specific associations may also yield more stable and predictable benefits when compared with facultative conditional mutualisms, where the actual protection arising for the trophobionts may depend strongly on population density, enemy pressure, or species of attendant ant (Bristow 1984, Cushman & Whitham 1989).

However, to specialize on one host ant genus or species is also associated with considerable costs. The survival of an obligate myrmecophile is entirely dependent on the availability of its host ant, and fluctuations in the abundance of the host or even local extinctions severely affect the fate of such specialized lycaenids. *Maculinea arion*, for example, became extinct within a few years after the populations of its host ant *Myrmica sabuleti* had strongly declined in southern England due to habitat deterioration (Thomas 1989).

Many more populations of this and other *Maculinea* species with a similar life-cycle are now in great danger of extinction (e.g. Elmes & Thomas 1987), the close association with specific ants strongly limiting the ability of such species to react to environmental changes.

As a rule, most lycaenids whose larvae have tight and specific associations with ants only occur in highly isolated and fragmented populations (e.g. Smiley et al. 1988), or they do exist even in single colonies in an extremely limited area (e.g. many Aphnaeini and *Lepidochrysops* species in Africa: Henning 1984a, 1987b; *Acrodipsas illidgei, Paralucia pyrodiscus* in Australia: Samson 1987, 1989, Braby 1990).

Furthermore, obligate myrmecophiles may become unattractive to, or may even be attacked by, non-host ant species if the latter take the specific signals (pheromone mimics) of the caterpillars as an indication for the presence of competing and hostile alien ants. Samson & O'Brien (1980) and Pierce (1989) have reported that *Ogyris* and *Jalmenus* caterpillars are preyed upon by ants other than their usual hosts (see also Malicky 1961).

Accordingly, specific ant-associations should be less advantageous in areas with a highly diverse ant fauna, where the predictability to encounter the particular host ant taxon is low, whereas the risk of being preyed upon by inadequate non-host ants is high.

Obligatorily myrmecophilous lycaenids may further face with severe nutritional constraints. In obligate mutualisms there is a distinct selective pressure towards extremely high food rewards for attendant ants. *Anthene emolus* caterpillars exhibit extraordinarily high DNO secretion rates (Fiedler & Maschwitz 1989b; see also the permanent exudation of DNO secretions in some Aphnaeini), and in *Jalmenus evagoras* ant-attendance results in lower pupal weight and fecundity (Pierce et al. 1987, Elgar & Pierce 1988).

As a consequence the quality of larval nutrition achieves paramount importance (Baylis & Pierce 1991), and any shortage of food may become critical for the maintainance of ant-associations and hence for survival. Thus, less favourable or unpredictable food resources of lycaenid caterpillars may select against the evolution of obligate mutualisms. And secondly, if ants are used as oviposition cues, this either leads to a distinct reduction of the proportion of potential hostplants that can actually be utilized, or it forces the caterpillars to accept a wide array of plant species (Pierce & Elgar 1985).

So, physiological limitations in the potential to evolve polyphagy could pose severe constraints against those obligatory ant-associations that are based on large amounts of nutritive liquids.

Obligate and tight ant-associations are thus by no means generally advantageous when compared with facultative mutualisms, and one can formulate the following criteria for the evolution of obligate and specific myrmecophily in the Lycaenidae:

1.) Ecologically dominant ant species with highly predictable occurrence (e.g. long-lived colonies) are the preferred hosts.
2.) Obligate myrmecophily normally arises in lycaenid taxa whose larvae search shelter in ant nests for roosting, pupation or diapause.
3.) A permanently high enemy pressure reinforces the evolution of obligate associations.
4.) Caterpillars that prey upon ant brood always need (and have) specific host ants.

As a corollary conditions can be exemplified where obligatory myrmecophily should rarely evolve:

1.) Rare ant species or ants with very small colonies are unlikely hosts of obligate myrmecophiles.
2.) Regions with a depauperate ant fauna (islands, high latitudes or altitudes) rarely house obligatorily myrmecophilous lycaenids.
3.) In tropical rainforests with their extremely diverse ant fauna relatively fewer obligate myrmecophiles are expected, since there the predictability of finding the adequate hosts is lower.
4.) Widely distributed lycaenids, or species occurring in a broad range of ecological conditions, have a low likelihood of specializing towards one particular host ant.

These criteria could partly explain the zoogeographical pattern that obligate myrmecophily is common in Australia and South Africa, less common in the wet tropics and rather rare in the temperate regions. Tropical rain forests with their extraordinarily diverse ant fauna (Hölldobler & Wilson 1990) provide rather few trophobiotic ant species whose occurrence is sufficiently predictable to support the evolution of obligate myrmecophily.

One of the few exceptions is the dominant genus *Oecophylla*, and this ant indeed houses several obligatorily myrmecophilous lycaenids. In contrast, the risk of en-

countering inadequate hostile ants, or the risk not to find the appropriate combination of hostplants and host ants, is rather high in these most species-rich terrestrial habitats.

In subtropical, seasonally dry habitats a less diverse ant fauna with distinctly dominant species exists. Likewise, the flora is less diverse with some species dominating the vegetation. In such areas lycaenid caterpillars derive considerable protection and microclimatic benefits from visiting ant nests during day time or dry seasons, and the enemy pressure during the short active period of larvae must be considered to be rather high (see Pierce et al. 1987 for an Australian species).

All these factors, in concert, should have promoted the evolution of obligate ant-associations, and in fact the highest proportions of obligate myrmecophiles occur in areas matching the above conditions (Australia and South Africa). Once such an association has been established, the fragmentation and isolation of the populations may subsequently lead to speciation, and the large species diversity of the Aphnaeini genera *Spindasis, Aloeides*, and *Poecilmitis*, or of the polyommatine genus *Lepidochrysops* undoubtedly evolved in this way.

In temperate zones (e.g. Holarctic region), obligate associations are rather rare. The generally lower diversity of ants and lycaenids, the presumably lower selective pressure exerted by parasitoids and predators, the often highly fluctuating and unpredictable climatic conditions, and the restricted activity periods of lycaenids and ants obviously did not favour the evolution of specific and obligate associations in a greater number of species.

Clearly the evolution of obligate myrmecophily has also a historical and taxonomical dimension. Historically, the evolution of obligate symbioses requires sufficient time to allow the accumulation of the adaptations required. The extermination of large parts of the Holarctic lycaenid fauna due to repeated glaciations has certainly restricted or cut off the evolution of more numerous obligatory ant-associations. In tropical and subtropical regions, in contrast, evolution was not as totally interrupted, albeit considerable climatic deteriorations have occurred there as well.

Taxonomically, the rise of obligate ant-associations is restricted to certain subgroups of the Lycaenidae (this study), and this has two possible reasons. First, the potential to evolve specific ant-associations is not equally available in all taxa. For example, secondarily myrmecoxenous lycaenids, which have reduced or lost their ant-organs and ant-associations, are less likely to evolve specific myrmecophily again (Thecliti, Lycaenini).

Secondly, once a lycaenid species has attained obligate myrmecophily, it is likely that its phylogenetic descendents retain or further modify this character. As with the hostplant relationships, a distinct phyletic conservatism must be expected.

The mechanisms engaged in obligatory myrmecophily (recognition of host ants, production of specific chemicals) further pose distinct barriers against random shifts in the host ants used. Accordingly, whole genera can be characterized by their obligate myrmecophily, and all more or less subtle specific differences regarding myrmecophily within these genera must be viewed as secondary adaptations during speciation (e.g. *Spindasis, Phasis, Poecilmitis, Acrodipsas, Maculinea, Lepidochrysops*).

In other genera (e.g. *Aloeides, Hypochrysops, Ogyris, Jalmenus*), the evolution of obligate myrmecophily seems to have occurred in parallel several times starting from similar preconditions (steadily myrmecophilous larvae), but this view may well be modified if more is known about the phylogeny and behavioural ecology of the respective taxa.

Interestingly, there is yet no evidence that a reverse evolution from obligatory towards facultative myrmecophily has ever occurred within the Lycaenidae, although such would be possible from theory. Apparently, obligate myrmecophily is mostly an evolutionary "one-way road" leading to ever increasing specialization, and it has been followed by a rather limited number of lycaenid genera. Only a few of these were distinctly successful in terms of species number, area of distribution, or abundance in their habitats, while in other lineages the obligatory myrmecophiles remained a small minority.

To the end of this discussion of obligate myrmecophily, some of the better known examples shall be shortly visited under an evolutionary view.

1.) Aphnaeini: As a whole this tribe is characterized by its tight relationships to ants, and a close association with *Crematogaster* (Myrmicinae) may well belong to its groundplan. Deviations occur in the monophyletic group *Aloeides/Erikssonia* (always associated with *Acantholepis* [Formicinae]) and in *Axiocerses amanga* and *Poecilmitis pyroeis* (with *Camponotus* [Formicinae]). Records of *Spindasis* or *Axiocerses* with *Pheidole* require confirmation.

This implies that major host shifts (even across ant subfamilies) are possible, but they either occur only in single cases (*Axiocerses, Poecilmitis*), or they give rise to a new radiation (*Aloeides*). Clearly, the host ant relationships of obligatorily myrmecophilous lycaenids are not basically coincidental, but largely follow phyletic patterns.

2.) Luciiti: Tight relationships to the ant genus *Iridomyrmex* (Dolichoderinae) are characteristic for this subtribe. Primarily these associations were probably not obligatory (as it is still the case with *Pseudodipsas* or several *Hypochrysops* species), and a few *Hypochrysops* species and the *Philiris* lineage of the *Hypochrysops* section have even reduced this myrmecophily. *Lucia, Paralucia*, *Acrodipsas*, and several *Hypochrysops* species have evolved obligate ant-associations in parallel.

Again major host shifts across ant subfamilies have occurred (to *Notoncus* [Formicinae] and at least twice to *Crematogaster* [Myrmicinae]), even within the genus *Acrodipsas* whose larvae are predators of ant-brood. Nevertheless, obligate myrmecophily and host ant use in the Luciiti show a distinct taxonomic pattern.

3.) *Ogyris* and *Jalmenus*: Judging from the data given by Atsatt (1981b) and Common & Waterhouse (1981) some *Ogyris* species are facultatively myrmecophilous and largely associated with Dolichoderinae ants (*Iridomyrmex, Froggatella, Technomyrmex*), including at least one obligatorily myrmecophilous species, *Ogyris amaryllis*. Another group of species is associated with the Formicinae genus *Camponotus*, again containing some obligate myrmecophiles.

It is not yet known whether this pattern, starting from facultative associations, is due to an early dichotomy towards *Camponotus* or *Iridomyrmex* as host ants, or whether first obligate myrmecophily evolved, followed by a later shift in the host ant genus utilized.

The genus group *Jalmenus/Pseudalmenus* is associated with Dolichoderinae ants (mainly *Iridomyrmex*, also *Froggatella*), suggesting an ancestral adaptation to this peculiar ant group. Several species have, perhaps independently, transcended the stage of steady, but facultative myrmecophily and now maintain obligate mutualisms.

4.) *Maculinea*: This small genus of the *Glaucopsyche* section is closely related to *Iolana* and *Glaucopsyche*. The latter, in particular, is highly myrmecophilous with species from the genus *Myrmica* among its attendant ants. *Glaucopsyche* larvae sometimes pupate in ant nests (Tilden 1947). It seems feasible that the *Glaucopsyche*-like ancestor of today *Maculinea* first regularly entered into ant nests for pupation and diapause. Then, probably, a shift from pupal (typical for species of the *Glaucopsyche* section) to larval diapause occurred.

Since *Myrmica* is one of the few Holarctic ant genera that have brood throughout the year, only larvae hibernating in colonies of this genus could additionally use ant grubs as food resource, perhaps in response to shortages in plant food (climatic constraints during the ice ages?). This selected for a specialization upon *Myrmica* ants as hosts with the evolution of the associated adoption and integration mechanisms.

Finally, the most advanced species (*M. alcon, M. rebeli*) even shifted from brood predation to solicitation of trophallactic regurgitations, thus more effectively utilizing the ant colonies as food resource.

5.) *Lepidochrysops*: The closest relatives of this genus are the mainly African *Euchrysops* species that are facultatively myrmecophilous. *Camponotus* ants are well represented among the attendant ants of *Euchrysops* larvae, and *Eu. dolorosa* appears to be somewhat specialized to *Camponotus niveosetosus* chemically (Henning 1983b). In *Lepidochrysops*, *Camponotus* became the exclusive host ants. Some species usually referred to as *Lepidochrysops* (*lacrimosa, ariadne*?) are still facultative myrmecophiles with entirely herbivorous larvae (Clark & Dickson 1971).

The remaining species shifted to Lamiaceae/Selaginaceae (with few secondary extensions) and became brood predators of two peculiar *Camponotus* species. As within the *Maculinea-Glaucopsyche* group the larval period of these *Lepidochrysops* species is distinctly longer than in their phytophagous relatives. This suggests that again a shift towards larval diapause in ant nests (perhaps as a response to escape dry seasons?) may have been a decisive step in the evolution of carnivory in the *Lepidochrysops* section.

Secondary myrmecoxeny

Reductions of myrmecophily have repeatedly occurred, and most of these instances can be related to three factors: larval hostplants, feeding habits, and habitat. While apparently none of these factors is alone suffcient to favour secondary myrmecoxeny, a combined incidence of two or more of them has obviously selected against ant-associations.

H o s t p l a n t s — As has been discussed above, myrmecoxeny largely occurs in lycaenids whose larvae are food specialists on, for lycaenid larvae, "unusual" hostplants. *Philiris* on Lauraceae, Moraceae, or Euphorbiaceae, Thecliti on Hamamelididae or Oleaceae, *Eumaeus* on cycads, or *Agriades* on Primulaceae provide examples. Possibly, the association of Lycaenini caterpillars with Polygonaceae (that often contain high amounts of oxalic acid) have also played a role in the loss of true myrmecophily.

Such hostplants may be nutritionally inferior, although ant-associations are known from other lycaenids feeding on the same plant taxa. Furthermore, the myrmecoxenous food specialists may derive some protection from secondary plant compounds that render them unpalatable for predators (proven for *Eumaeus*: Bowers & Larin 1989, Bowers & Farley 1990; feeding experiments with *Lycaena tityrus* larvae offered to *Leptogenys* and *Pseudomyrmex* ants also suggest unpalatability: Fiedler, unpublished).

Generally, the comparative survey of more than 1000 lycaenid species supports the notion that specific associations with deviating hostplants favour reductions of myrmecophily, albeit this trait is by far not universal.

F e e d i n g h a b i t s — Caterpillars with endophytic life-habits (e.g. fruit-borers) are often myrmecoxenous. At a first stage the development of the TOs is delayed (*Leptotes*), or they are completely reduced (*Cupido, Iolana, Deudorix, Capys*, Hypolycaeniti, Eumaeiti). Reductions of the TOs are likewise common in species whose larvae live in ant nests (*Acrodipsas, Maculinea, Lepidochrysops*), suggesting that the function of these organs becomes insignificant in hollow spaces and cavities.

As a next step the DNO may be totally reduced (*Artipe, Bindahara, Cacyreus*). Typically, flower- or fruit-boring lycaenid larvae are rarely or never visited by ants. Endophytism thus proves a well-founded alternative defence strategy that partly renders myrmecophily superfluous. However, several endophytic larvae still retain a DNO and at least weak ant-associations (e.g. *Hypolycaena, Leptomyrina, Deudorix, Everes* etc.).

H a b i t a t — Habitats with a depauperate ant-fauna favour secondary myrmecoxeny. The Hawaii islands have no native ant species, and the endemic *Udara blackburni* (Polyommatini) has in fact neither a DNO nor TOs (Scott 1986). Most Thecliti mainly occur in the canopy of temperate zone deciduous forests, and Jeanne (1979), Fellers (1987, 1989) and Weseloh (1989) have provided evidence that the selective pressure arising from predatory ants is distinctly lowered in such habitats.

A reduced abundance and diversity of ants implies a lower chance of maintaining stable ant-associations and its related potential benefits, and it thus may have supported the loss of ant-organs in the ancestor of the subtribe Thecliti.

The ant-fauna of arctic or alpine tundras is extremely impoverished, and unsurprisingly several lycaenids specialized to these habitats are secondarily myrmecoxenous (*Agriades, Vacciniina optilete*). A similar altitudinal trend was noted for ant-associations of membracids (Olmstead & Wood 1990b).

In summary, judging from a global survey of life-histories, certain traits select against the maintenance of ant-associations, although none of these is at the same time

necessary and sufficient. In various taxa the mechanisms selecting for secondary myrmecoxeny are not even marginally understood (e.g. Lycaenini).

The lability of lycaenid myrmecophily in evolutionary time is perhaps less pronounced than previously postulated (e.g. Kitching & Luke 1985, Pierce 1987), but certainly the local selective "environment" of a given caterpillar species is ultimately decisive as to whether the benefits of myrmecophily outweigh its costs.

A more detailed understanding of the selective forces favouring secondary myrmecoxeny requires a more complete knowledge of the respective species, and clearly the study of lycaenid myrmecophily will decidedly profit from investigations that include myrmecoxenous caterpillars.

Species diversity of the Lycaenidae: is myrmecophily a part of the answer?

It has repeatedly been suspected that the relationships between lycaenids and ants have supported the radiation of the former (e.g. Ehrlich & Raven 1964, Vane-Wright 1978, Cottrell 1984), but only one study has attempted to exemplify how ant-associations could amplify the species diversity (Pierce 1984). She suggested two possible scenarios:

a) If lycaenid females oviposit in the presence of specific host ants, "oviposition mistakes" on non-hostplants may occur more often than in other butterflies only responding to plant chemistry when egg-laying. Although most such oviposition mistakes do not result in a successful amplification of the hostplant range, at least a few cases will do so. Given the postulated greater absolute frequency of these mistakes in lycaenids, there should exist a significant potential pathway towards adaptation to new hostplants and diversification, eventually resulting in speciation.

b) If lycaenids require a combination of both specific host ants and food plants, their populations should occur more patchily than in most other butterflies. Accordingly, the isolation of such demes more likely favours speciation, even more so since most lycaenids are not migratory.

Available evidence supports both hypotheses. At least some species lay eggs on a broad range of plants merely in the presence of appropriate ants, and many closely ant-associated species have extremely fragmented populations (e.g. Pierce 1984, Henning 1987b, Elmes & Thomas 1987, Smiley et al. 1988). However, ant-dependent oviposition is restricted to, but is not even universal among, obligatory myrmecophiles, and the majority of obligatorily myrmecophilous lycaenids are food specialists (see above).

Furthermore, a combination of specific hostplants and host ants is again only important for obligate myrmecophiles, and evidence has been presented above that these probably account for less than 20 % of the extant species diversity of the Lycaenidae. So, albeit the two scenarios presented by Pierce (1984) hold true for some specialized lycaenid groups, they cannot generally explain the great diversification of this family.

Further objections additionally qualify the general validity of both hypotheses. As already emphasized by Chew & Robbins (1984), the widest hostplant ranges are observed in lycaenids that are specialized on flowers or fruits (see also this study). Probably,

egg-laying on immature plant tissues with presumably lower contents of secondary compounds increases both the likelihood of oviposition mistakes and the probability that the actual substrate can be consumed by the emerging larvae.

However, flower- and fruit-feeding is by no means restricted to highly myrmecoxenous caterpillars, but is indeed most widespread among caterpillars with low-level ant-associations. Especially some Eumaeiti genera (*Callophrys, Strymon*; see also Fiedler 1990d) heavily utilize flowers, and the hostplant ranges of these mostly myrmecoxenous genera are remarkable, including conifers and monocots.

Therefore, the hostplant diversification pathway via flower- or fruit-feeding is certainly a very important one for the evolution of the Lycaenidae, but it is by no means restricted to, or best developed among, obligatory myrmecophiles. Rather, there is a taxonomic pattern: this mechanism is most important in taxa with a distinct overall preference for inflorescences (e.g. Deudorigiti, Eumaeiti, Polyommatini), irrespective of myrmecophily.

Atsatt (1981b) and Pierce (1984) also stated that host shifts among food plants should be more easy to achieve via oviposition mistakes than shifts between host ants. The conservative association of numerous obligatory myrmecophilous genera with one host ant genus each (most Aphnaeini, *Lepidochrysops, Maculinea*) supports this view, but significant exceptions even across ant subfamilies do exist (*Hypochrysops, Acrodipsas, Poecilmitis*; see above). Thus, although certainly a rare event, successful major host ant shifts are possible.

With regard to the "speciation through fragmentation" scenario, it seems feasible that the high number of locally endemic species in African genera such as *Aloeides, Poecilmitis* and related Aphnaeini, or the species-diversity of *Lepidochrysops* have evolved as a consequence of extreme fragmentation of populations, and several of these taxa are known only from single colonies (Henning 1987b). A similar situation may be prevalent among some Australian Luciiti or Zesiiti.

Populations of the Holarctic *Plebejus idas* (specifically associated with certain *Formica* ants) and of the Palaearctic *P. argus* (associated with *Lasius* species) are typically very localized, and these two species might diverge into new species in the course of evolution (both are yet subdivided in numerous morphologically distinct subspecies).

Other obligate myrmecophiles, however, have huge distributions. Several *Maculinea* species occur through large parts of the Palaearctic region (*M. arion, M. teleius, M. alcon*), but there is little evidence that their localized populations (that are often referred to as "subspecies") differ more markedly than populations of non-myrmecophilous species covering a comparable range. *Liphyra brassolis* occurs from India to Australia with only minor geographic variation.

Furthermore, highly localized popualtions exist in many facultatively myrmecophilous and myrmecoxenous species. The subgenus *Agrodiaetus* in the *Polyommatus* group offers an excellent example of an explosive radiation in the circum-Mediterranean region and West Asia. Typically, *Agrodiaetus* taxa differ little except in chromosome numbers.

Another example for highly fragmented allopatric population groups is provided by the Eurasiatic subgenus *Plebejides* (Bálint & Kertész 1990). Both *Agrodiaetus* and *Plebejides* are closely, but unspecifically associated with ants, and there is no evidence that factors other than historical changes in the climate and availability of hostplants have promoted isolation and speciation (see Bálint 1991 for *Plebejides*). Examples of myrmecoxenous lycaenids with isolated and fragmented populations in parts of their distribution area are *Lycaena helle* and *L. dispar.*

Thus, fragmentation of populations, geographical isolation, and subsequent (not necessarily allopatric) specialization to novel hostplants are the most important speciation processes among myrmecoxenous and facultatively myrmecophilous lycaenids, as well as among obligate myrmecophiles. In the latter, fragmentation may be enhanced, and hostplant changes might occur more often in certain subgroups in response to specific ant-associations, as suggested by Pierce (1984).

Given the restricted number of obligate myrmecophiles, these processes can at best explain the evolution of species diversity in taxa such as Aphnaeini, Luciiti, Zesiiti, or the *Lepidochrysops* section. For the remaining majority of the extant Lycaenidae, there is at present no evidence that and how ant-associations could have promoted speciation directly.

The impressive species-richness of the Lycaenidae as a whole suggests that myrmecophily has indeed played an important role. Most likely, the generalized notion that ant-association offers an important adaptive zone ("enemy-free space") with limited competition of related herbivores (i.e. other butterfly caterpillars), in combination with higher survival rates of myrmecophilous larvae, are sufficient explanations for the evolutionary success of the Lycaenidae. In terms of hostplant specializations and total species diversity, the Nymphalidae have distinctly overtaken the Lycaenidae.

Concluding remarks

The present study is an attempt to combine experimental and life-history data with morphological, systematic, zoogeographical and ecological traits. Besides making accessible the scattered information on more than 1000 lycaenid species, it was intended to demonstrate that comparative methods combined with attempts to understand the phylogeny are crucial to achieve a more detailed view of evolution.

Experimental data and theoretical considerations strongly require to be supplemented from the fund of organismic and descriptive biology. Unfortunately, the phylogeny of the Lycaenidae is not yet sufficiently worked out to allow more rigid quantitative analyses and predictions (cf. Harvey & Purvis 1991). However, since the comparative method has generally turned out to yield significant results even if the underlying phylogeny is not completely resolved, the hypotheses discussed here should provide a reasonable basis for further studies.

The ant-associations of the Lycaenidae are perhaps the best-known paradigm of myrmecophilous interactions, and continued investigations seem especially rewarding.

The documentation of further life-history data of today under-represented taxa (especially from the tropics), the sampling of additional experimental data on the chemistry of myrmecophilous secretions and on the details of behavioural interactions, and, with high priority, a more complete phylogenetic analysis must now continue. Then, a synthesis of classical biology, experimental ethology and ecology, and theoretical sociobiology and evolutionary biology will be attained.

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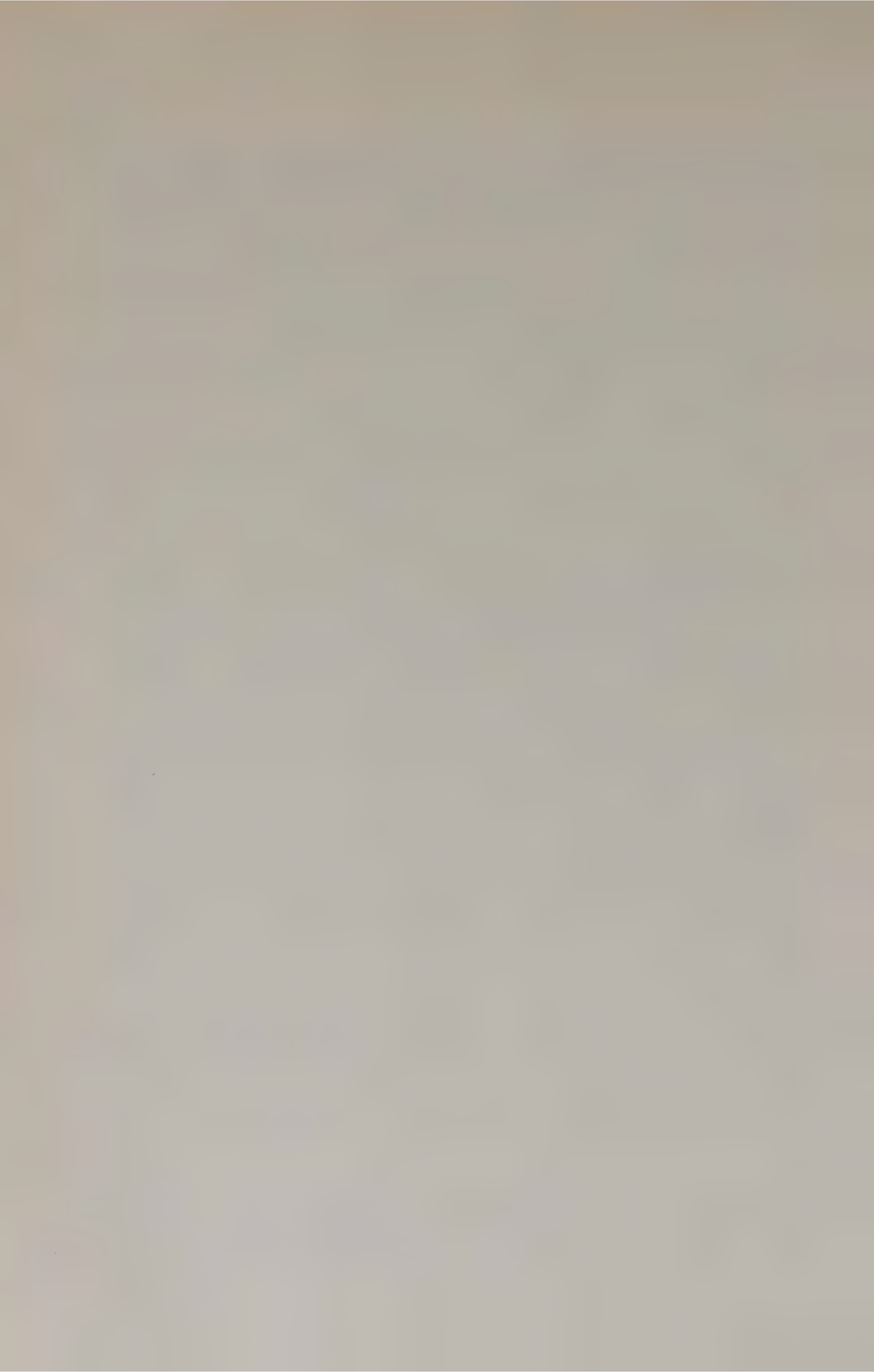
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APPENDIX: TABLES 17-19

Table 17: This table summarizes all information traced concerning larval food substrates, host-range indices, preferences for protein-rich hostplant tissues, and data regarding the presence of myrmecophilous organs and/or ant-associations for more than 1000 lycaenid species.

First column: Species arranged according to the higher classification adopted throughout this work. Nomenclature and taxonomy largely follow Bridges (1988), but deviate where more recent revisions are available. When the original records were published under a different species name (synonyms, misidentifications), this name is included in brackets in selected cases. Generic synonymies are omitted. Subspecies are generally not considered except a few cases where the taxonomic status is uncertain. Subgenera are given to facilitate use, if these are regularly treated as distinct genera as well.

Second column: Hostplant families (according to Ehrendorfer 1983), or other food substrates used by larvae. The first entry is usually the main hostplant taxon. The subsequent plant families are arranged in systematic order, the sequence not implying any preference hierarchies. In polyphagous species the listing starts with the legume families where appropriate. Questionable records are indicated by ?, highly doubtful data by ??. Where obvious from the sour-ces, laboratory data are designated with **lab**. Oviposition records (**ov.**) are only included when the respective substrate is likely to be the larval food.

Third column: Host-range indices. 1 : monophagous (1 hostplant species); 2 : stenoligophagous (1 hostplant genus); 3 : oligophagous (1 hostplant family); **4** : moderately polyphagous (2 hostplant families); 5 : polyphagous (3+ hostplant families). Very closely related plant families are treated as one taxon for these indices (e.g. the legume families Mimosaceae, Caesalpiniaceae and Fabaceae; Lamiaceae and Selaginaceae). Tentative assignments are followed by ?. Entirely non-herbivorous species (e.g. Liptenini, Miletinae) are excludeded (-). A question mark ? alone indicates that, based on the literature evaluated, no categorization is possible at present.

Fourth column: Preferences for presumed protein-rich hostplant parts. **y** : preference for young growth/buds; **i** : preference for inflorescences; **f** : preference for fruits or seed capsules; **e** : larvae with (at least partially) endophytic life-habits. **-** : no such preferences recorded. Assignments in parentheses () are hypothetically derived from closely related species. A question mark ? indicates that, based on the literature evaluated, no categorization is possible at present.

Fifth column: Degree of myrmecophily (as defined in Fiedler 1991) and presence of myrmecophilous organs. All records refer to older larvae except where stated otherwise. **0** : myrmecoxenous (not associated with ants in the field); 1 : weakly myrmecophilous (only casual and instable ant-associations); 2 : moderately myrmecophilous (ant-associations regularly occur at least with part of the larvae); 3 : steadily myrmecophilous (almost all older larvae are nearly permanently attended by ants); 4 : obligatorily myrmecophilous (caterpillars are dependent on ants: obligatorily mutualistic or parasitic larvae). ** : larvae with DNO and TOs present; * : only DNO present; T : only TOs present; no symbol: only PCOs. Symbols in parentheses () refer to hypothetical assignments based on closely related species. Doubtful data are followed by ?. A question mark ? alone indicates that, based on the literature evaluated, no categorization is possible at present.

Sixth column: Selected references. A full bibliography would have been impossible, especially for many Holarctic species.

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Poritiinae:					
Poritiini:					
Poritia erycinoides	Fagaceae	2?	?	0	Rosier 1951
Liptenini:					
Pentiliti					
Alaena amazoula	Lichen	-	-	0	Migdoll 1988
A. margaritacea	Lichen	-	-	0	Clark & Dickson 1971
A. nyassa	Lichen (ov.) Poaceae ??	-	-	(0)	Kielland 1990, Ackery & Rajan 1990
A. caissa	Lichen ?	-	-	(0)	Kielland 1990
A. subrubra	Anacardiaceae ??	-	-	(0)	Ackery & Rajan 1990
Pentila tropicalis	Lichen	-	-	0	Migdoll 1988
P. inconspicua	Lichen ?	-	-	(0)	Kielland 1990
P. rogersi	Lichen ?	-	-	(0)	Kielland 1990
P. rondo	Lichen ?	-	-	(0)	Kielland 1990
Telipna erica consanguinea	Lichen	-	-	0	Jackson 1937
T. sanguinea	Lichen	-	-	0	Jackson 1937
Ornipholidotos muhata	Lichen	-	-	0	Jackson 1937, van Someren 1974
Durbaniiti					
Durbania amakosa	Cyanobacteria	-	-	0	Henning 1983a
D. limbata	Lichen	-	-	0	Migdoll 1988
D. saga	Lichen	-	-	0	Clark & Dickson 1971
Cooksonia neavei	Lichen	-	-	0	Pennington et al. 1978
C. aliciae	Lichen	-	-	0	Ackery & Rajan 1990
Lipteniti					
Mimacraea krausei	Lichen	-	-	0	Jackson 1937
M. marshalli	Lichen	-	-	0	Stempffer 1967
M. skoptoles	Lichen (ov.)	-	-	(0)	Kielland 1990
M. poultoni	Lichen	-	-	(0)	van Someren 1974
Citrinophila tenera	Lichen ?	-	-	0	Farquharson 1922
C. erastus	Lichen ?	-	-	(0)	Kielland 1990
Teriomima zuluana	Lichen	-	-	0	Migdoll 1988
T. micra	Lichen (ov.)	-	-	(0)	Kielland 1990
T. subpunctata	Lichen (ov.)	-	-	(0)	van Someren 1974
T. parva	Lichen (ov.)	-	-	(0)	Kielland 1990
Euthecta cooksoni	Lichen (ov.)	-	-	(0)	Kielland 1990
Baliochila aslauga	Lichen Fabaceae ??	-	-	0	Migdoll 1988
B. hildegarda	Lichen	-	-	0	Sevastopulo 1975
B. dubiosa	Lichen (ov.)	-	-	(0)	van Someren 1974
B. fragilis	Lichen (ov.)	-	-	(0)	van Someren 1974
B. minima	Lichen (ov.)	-	-	(0)	van Someren 1974
B. stygia	Lichen (ov.)	-	-	(0)	van Someren 1974
Cnodontes vansomereni	Lichen (ov.)	-	-	(0)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Eresina corynetes	Lichen ?	-	-	0	Farquharson 1922
Eresinopsides bichroma	Lichen ?	-	-	(0)	Kielland 1990
Mimeresia libentina	Lichen (ov.)	-	-	(0)	Ackery & Rajan 1990
Liptena undina	Lichen	-	-	0/4?	Jackson 1937
Teratoneura isabellae	Lichen	-	-	0/4?	Farquharson 1922
Iridana incredibilis	Lichen	-	-	0	Jackson 1937
I. perdita marina	Lichen	-	-	0/4?	Jackson 1937
Deloneura millari	Lichen ?	-	-	0	Migdoll 1988
+ ssp. *sheppardi*	Lichen ? Fabaceae ??	-	-	0	Clark & Dickson 1971
D. ochrascens	Lichen (ov.)	-	-	0/4??	Jackson 1937, van Someren 1974, Kielland 1990
D. subfusca	Lichen ?	-	-	(0?)	Kielland 1990
Epitola (Aethiopana) honorius	Lichen	-	-	3?	Farquharson 1922
E. (Epitola) concepcion	Lichen	-	-	0	Farquharson 1922
E. hewitsoni	Lichen	-	-	0	Farquharson 1922
E. miranda	Lichen	-	-	0	Farquharson 1922
E. urania	Lichen	-	-	0/3?	Jackson 1957
E. carcina	Lichen ?	-	-	3?	Ackery & Rajan 1990
E. catuna	Lichen	-	-	3	van Someren 1974
E. ceraunia	Lichen ?	-	-	3?	Ackery & Rajan 1990
E. cercene	Lichen	-	-	3	van Someren 1974
E. elissa	Lichen ?	-	-	3?	Ackery & Rajan 1990
E. kamengensis	Lichen	-	-	3	van Someren 1974
Hewitsonia similis	Lichen	-	-	0	Farquharson 1922
H. kirbyi	Lichen	-	-	0	Jackson 1937
H. crippsi	Lichen ?	-	-	0	Jackson 1947
Miletinae:					
Miletini:					
Spalgiti					
Spalgis epeus	Coccidae	-	-	0	Cottrell 1984
Sp. lemolea	Coccidae Pseudococcidae	-	-	0	Cottrell 1984
Feniseca tarquinius	Pemphigidae	-	-	0	Scott 1986, Klassen et al. 1989
Tarakiti					
Taraka hamada	Hormaphididae + honeydew + siphon secretions	-	-	0	Cottrell 1984, Banno 1990
Miletiti					
Miletus chinensis	Aphidoidea	-	-	0/3?	Cottrell 1984
M. boisduvali	Aphidoidea Coccidae	-	-	0/3?	Cottrell 1984

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Miletus biggsii	Hormaphididae	-	-	0/4?	Maschwitz et al. 1988
	Coccidae				
M. symethus	Coccidae	-	-	0/4?	Eliot 1980
	Dolichoderus brood ?				
M. nymphis	Coccidae	-	-	(0/3?)	Maschwitz et al. 1988
Allotinus unicolor	Hormaphididae	-	-	0/3?	Maschwitz et al. 1985a,
	Psyllidae ?				Fiedler & Maschwitz 1989c
	Membracidae ?				
A. subviolaceus	Membracidae	-	-	0	Maschwitz et al. 1985a
A. major	Membracidae	-	-	0	Kitching 1987
A. davidis	Aphidoidea	-	-	0	Maschwitz et al. 1985a
A. substrigosus	Hormaphididae	-	-	0	Maschwitz et al. 1988,
					Schütze 1990
A. apries	Coccidae (L1)	-	-	4?	Maschwitz et al. 1988
	Myrmicaria brood ?				
Logania malayica	Hormaphididae ?	-	-	0?	Maschwitz et al. 1988
Megalopalpus zymna	Membracidae	-	-	0	Cottrell 1984
	Jassidae				
Lachnocnemiti					
Lachnocnema bibulus	Jassidae	-	-	0/4?	Cripps & Jackson 1940,
	Membracidae				van Someren 1974,
	Psyllidae				Cottrell 1984
	+ honeydew + *Camponotus* regurgitations				
L. brimo	Membracidae	-	-	0?	Ackery 1990
	Psyllidae				
L. durbani	Coccidae (lab)	-	-	0?	Ackery & Rajan 1990
	Membracidae (lab)				
Thestor dicksoni	*Anoplolepis* brood ?	-	-	4	Clark & Dickson 1971
Th. basutus	Psyllidae (L1-L3)	-	-	4	Clark & Dickson 1971
	Anoplolepis brood ?				
Th. obscurus	Ant brood ?	-	-	4?	Claassens & Dickson 1980
Th. brachycerus	Ant brood ?	-	-	(4?)	Clark & Dickson 1971
Th. dukei	Ant brood ?	-	-	(4?)	Clark & Dickson 1971
Th. rileyi	Ant brood ?	-	-	(4?)	Clark & Dickson 1971
Th. holmesi	Ant brood ?	-	-	4	Clark & Dickson 1971
Th. protumnus	Coccidae	-	-	(4?)	Clark & Dickson 1971,
	Ant brood ?				Migdoll 1988
<u>Liphyrini</u>:					
Euliphyra mirifica	*Oecophylla* regurgitations		-	4	Hinton 1951, Dejean 1991
	+ prey items of host ants				
Eu. leucyania	*Oecophylla* regurgitations		-	4	Kielland 1990, Dejean 1991
	+ prey items of host ants				
Liphyra brassolis	*Oecophylla* brood	-	-	4	Johnson & Valentine 1986,
					Cottrell 1987
Aslauga lamborni	Membracidae	-	-	0^T	van Someren 1974,
	Coccidae				Cottrell 1984
A. purpurascens	Membracidae	-	-	0^T	Boulard 1968,
	Psyllidae (lab)				Cottrell 1981
	Coccidae (lab)				

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Aslauga latifurca	Membracidae	-		$0?^{T}$	Jackson 1937, Cottrell
	Coccidae				1981, Ackery & Rajan 1990
	Lycaenidae (lab)				
A. atrophifurca	Homoptera	-	-	$0^{T?}$	Cottrell 1984, Villet 1986
A. orientalis	Coccidae	-	-	(0^{T})	Cottrell 1981
A. vininga	Coccidae	-	-	$0?^{(T)}$	Cottrell 1984,
	Pseudococcidae				Ackery & Rajan 1990
Curetinae:					
Curetis thetis	Fabaceae	4	y, i	0^{T}	Hinton 1951
	Meliaceae				
C. regula	Fabales	3?	y	$0/2?^{T}$	DeVries 1984
C. felderi	Fabaceae	3	y	0^{T}	pers. obs.
C. santana	Fabaceae	3	(y, i)	0^{T}	Corbet & Pendlebury 1978
C. bulis	Fabaceae	3?	y	0^{T}	Eliot 1980
C. acuta	Fabaceae	3	(y)	0^{T}	Iwase 1954, Shirôzu &
					Hara 1974
+ ssp. *dentata*	Fabaceae	3	y	$(0)^{T}$	Johnston & Johnston 1980
Lycaeninae:					
Aphnaeini:					
Aphnaeus erikssoni	Convolvulaceae	2?	?	(4**)	Sevastopulo 1975
A. argyrocyclus	Euphorbiaceae	1?	?	(4**)	Sevastopulo 1975
A. orcas	Euphorbiaceae	5	?	(4**)	Sevastopulo 1975,
	Mimosaceae				Ackery & Rajan 1990
	Loranthaceae				
A. (Paraphnaeus)					
hutchinsoni	Loranthaceae	2/4?	e (galls)	4**	Jackson 1937,
	upon Mimosaceae				van Someren 1974
Spindasis ella	Mimosaceae	3	e	3/4**	Clark & Dickson 1971
	Fabaceae				
S. homeyeri	Mimosaceae	3	?	(3/4**)	Sevastopulo 1975,
	Caesalpiniaceae				Pennington et al. 1978
S. natalensis	Fabaceae	5	e	4**	Clark & Dickson 1971,
	Rubiaceae				Sevastopulo 1975
	Verbenaceae				
	Olacaceae ?				
S. victoriae	Mimosaceae	3	y	(3/4**)	Pennington et al. 1978
S. mozambica	Fabaceae	3	?	(3/4**)	Sevastopulo 1975
S. nyassae	Mimosaceae	3	y	4**	Hinton 1951,
	Fabaceae				Sevastopulo 1975
	+ *Crematogaster* regurgitations ?				
S. avriko	Mimosaceae	2?	y, e (galls)	4(**)	Ackery & Rajan 1990
S. tavetensis	Mimosaceae	2?	y, e (galls)	4(**)	Ackery & Rajan 1990
S. apelles	Anacardiaceae (ov)	2?	?	(4**)	van Someren 1974,
(+ ssp. *nairobiensis*)					Sevastopulo 1975
S. namaqua	Zygophyllaceae	2	?	4**	Henning 1983a
S. phanes	Olacaceae	2	?	4**	Henning 1983a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Spindasis lohita	Mimosaceae	5	?	3/4**	Corbet & Pendlebury 1978
	Proteaceae				
	Myrtaceae				
	Combretaceae, Santalaceae, Loranthaceae,				
	Convolvulaceae, Dioscoreaceae				
S. vulcanus	Rutaceae	5	?	3/4**	Pierce & Elgar 1985
	Sapindaceae				
	Rhamnaceae				
	Rubiaceae				
	Verbenaceae				
S. takanonis	Pinaceae	5	?	4**	Iwase 1955,
	Rosaceae				Pierce & Elgar 1985
	Elaeagnaceae				
	+ *Crematogaster* regurgitations				
Cigaritis zohra	Fabaceae	1	-	4**	Thomas & Mallorie 1985,
					Rojo de la Paz 1990
C. allardi	Fabaceae	4	-	3**	Thomas & Mallorie 1985,
	Cistaceae				Rojo de la Paz 1990
C. siphax	Cistaceae ??	?	?	(3/4**)	Devarenne 1990
C. (Apharitis)					
myrmecophila	Polygonaceae	1?	?	4**	Hinton 1951
C. (A.) acamas	Caesalpiniaceae ?	3?	?	4**	Larsen & Pittaway 1982
	Fabaceae ?				
	+ *Crematogaster* regurgitations, + *Crematogaster* brood ?				
Axiocerses tjoane	Mimosaceae	2	?	(4**)	Migdoll 1988
A. bambana (ssp.?)	Mimosaceae	3	?	4**	Clark & Dickson 1971
A. amanga	Olacaceae	4	-	3**	Jackson 1937,
	Mimosaceae				Sevastopulo 1975
A. harpax	Mimosaceae	2?	e (galls)	4**	Jackson 1947,
	+ *Crematogaster* regurgitations ?				Ackery & Rajan 1990
A. styx	Caesalpiniaceae	2?	?	(3**)	Sevastopulo 1975
A. (Desmolycaena)					
mazoensis	Mimosaceae	2	i	(3**)	Migdoll 1988
A. (Chloroselas)					
pseudozeritis	Mimosaceae	2	y	4**	Jackson 1937,
	+ *Crematogaster* regurgitations ?				van Someren 1974
Crudaria leroma	Mimosaceae	3	y	4**	Clark & Dickson 1971
Phasis thero	Anacardiaceae	4	e	4^T	Clark & Dickson 1971
	Melianthaceae (lab)				
Ph. braueri	Anacardiaceae	2	e	4^T	Clark & Dickson 1971
Ph. clavum	Anacardiaceae	2	e	4^T	Clark & Dickson 1971
Tylopaedia sardonyx	Ant brood ?	?	?	$(4*)^T$	Clark & Dickson 1971
Trimenia					
wallengrenii	Ant brood ?	?	?	$(4*)^T$	Clark & Dickson 1971
	Asteraceae (ov.)				
T. argyroplaga	Ant brood ?	?	?	$(4*)^T$	Clark & Dickson 1971
Argyrocupha					
malagrida	Ant brood ?	?	?	$(4*)^T$	Clark & Dickson 1971
	Fabaceae (ov.)				
	Asteraceae (ov.)				

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Aloeides thyra	Fabaceae	2	?	4(*)T	Claassens & Dickson 1980
A. pallida	Fabaceae (lab)	2	-	(4*)T	Clark & Dickson 1971
A. pierus	Fabaceae	2	?	3/4**	Claassens & Dickson 1980
A. depicta	Fabaceae (lab)	2	-	4**	Clark & Dickson 1971
A. gowani	Fabaceae (lab)	2	-	(4)**	Clark & Dickson 1971
A. clarki	Fabaceae (lab)	2	-	(4)**	Clark & Dickson 1971
A. aranda	Fabaceae (lab)	2	-	4**	Clark & Dickson 1971
A. henningi	Fabaceae (lab)	2	-	(4)**	Dickson 1953, Clark & Dickson 1971
A. trimeni	Sterculiaceae Fabaceae (lab)	2/4?	-	3**	Henning 1984
A. dentatis	Sterculiaceae	2	(i)	4T	Henning 1983a
A. damarensis	Fabaceae (lab)	2?	?	(4*)T	Clark & Dickson 1971
A. rossouwi	??	?	?	4(**)	Henning & Henning 1982
A. conradsi	??	?	?	4(**)	van Someren 1974
Erikssonia acraeina	Thymelaeaceae	1	-	4**	Henning 1984
Poecilmitis (Chrysoritis)					
zeuxo	Asteraceae	2?	-	(3)**	Clark & Dickson 1971
P. (Ch.) zonarius	Asteraceae	2?	-	(3**)	Claassens & Dickson 1980
P. (Ch.) cottrelli	Asteraceae	2?	-	(3**)	Pennington et al. 1978
P. (Poecilmitis)					
lycegenes	Anacardiaceae Ebenaceae Myrsinaceae	5	-	4**	Henning 1983a
P. lyncurium	Myrsinaceae ? Ebenaceae ?	4?	?	(4**)	Pennington et al. 1978
P. aureus	Euphorbiaceae	2?	?	4**	Henning 1983a
P. natalensis	Crassulaceae Asteraceae (lab?)	4	?	(4**)	Migdoll 1988
P. chrysaor	Crassulaceae Zygophyllaceae (lab) Anacardiaceae ?	5	-	4**	Dickson 1943
P. lycia	Crassulaceae	2?	-	(4**)	Pennington et al. 1978
P. felthami	Zygophyllaceae	2	-	4**	Clark & Dickson 1971
P. aridus	Asteraceae Zygophyllaceae (lab)	4	-	(4)**	Clark & Dickson 1971
P. pyroeis	Zygophyllaceae	2	-	4**	Clark & Dickson 1971
P. palmus	Bruniaceae Fabaceae Asteraceae Rubiaceae ?	5	-	3/4**	Clark & Dickson 1971
P. turneri	Zygophyllaceae (lab)	2?	?	(4**)	Dickson 1953
P. thysbe	Fabaceae Zygophyllaceae Asteraceae (lab)	5	y, i	4**	Clark & Dickson 1971
P. bamptoni	Zygophyllaceae Fabaceae Asteraceae	5	-	(4**)	Pennington et al. 1978
P. brooksi	Fabaceae	2?	?	4**	Henning 1987a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Poecilmitis pan	Asteraceae	2?	?	(4**)	Pennington et al. 1978
P. trimeni	Zygophyllaceae	2?	?	(4**)	Pennington et al. 1978
P. perseus	Zygophyllaceae	2?	?	4(**)	Pennington et al. 1978, Ackery & Rajan 1990
P. braueri	Zygophyllaceae	2	?	(4*)T	Clark & Dickson 1971
P. atlantica	Zygophyllaceae	2?	?	(4**)	Pennington et al. 1978
P. lysander	Zygophyllaceae Fabaceae (lab)	3?	-	(4)**	Clark & Dickson 1971
P. nigricans	Asteraceae Zygophyllaceae (lab)	4	y	4**	Clark & Dickson 1971
P. uranus	Fabaceae (lab) Zygophyllaceae (lab)	4	-	(4)**	Clark & Dickson 1971
P. adonis	Zygophyllaceae (lab)	3?	-	4**	Clark & Dickson 1971
P. kaplani	Asteraceae	1?	?	(4**)	Henning 1979
Oxychaeta dicksoni	*Crematogaster* brood	?	-	4(*)T	Clark & Dickson 1971
Lycaenini:					
Lycaena phlaeas	Polygonaceae	3	-	0	Ballmer & Pratt 1988, 1989
L. cupreus	Polygonaceae	2	-	0	Ballmer & Pratt 1988
L. nivalis	Polygonaceae	2	-	0	Ballmer & Pratt 1988
L. helloides	Polygonaceae Rosaceae	4	-	0	Ballmer & Pratt 1988
L. dorcas	Rosaceae Ericaceae ?	2/4?	-	0	Scott 1986
L. epixanthe	Ericaceae	1	y	0	Wright 1983
L. mariposa	Ericaceae	2	-	0	Ballmer & Pratt 1988
L. heteronea	Polygonaceae	2	y	2	Ballmer & Pratt 1988
L. gorgon	Polygonaceae	2	-	0	Ballmer & Pratt 1988
L. rubidus	Polygonaceae	2	-	2	Ballmer & Pratt 1988
L. xanthoides	Polygonaceae	2	-	2	Ballmer & Pratt 1988
L. editha	Polygonaceae	2	-	2	Ballmer & Pratt 1988
L. panava	Polygonaceae	2	-	(0)	Shields 1984
L. clarki	Polygonaceae	3	-	0	Clark & Dickson 1971
L. orus	Polygonaceae	2	-	0	Clark & Dickson 1971
L. dispar	Polygonaceae	2	-	0/1?	Hinton 1951, Duffy 1968
L. hyllus	Polygonaceae	3	-	0	Klassen et al. 1989
L. virgaureae	Polygonaceae	2	-	0	SBN 1987
L. ottomanus	Polygonaceae	2	-	0	Elfferich, pers. comm.
L. thersamon	Polygonaceae Fabaceae ??	3	-	0	Larsen & Nakamura 1983, Parker 1983, Schurian et al. 1991
L. phoebus	Polygonaceae Chenopodiaceae ?	3/4?	-	0	Devarenne 1990, Rojo de la Paz & Schurian, pers. comm.
L. asabinus	Polygonaceae ?	1?	-	(0)	Schurian & Hofmann 1982
L. tityrus	Polygonaceae	2	-	0	SBN 1987
L. alciphron	Polygonaceae	2	-	0	SBN 1987
L. hippothoe	Polygonaceae	2	-	0	SBN 1987
L. candens	Polygonaceae	2	-	(0)	Higgins & Riley 1978

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Lycaena hermes	Rhamnaceae	1	y	0	Ballmer & Pratt 1988
L. arota	Grossulariaceae	2	-	0	Ballmer & Pratt 1988
L. helle	Polygonaceae	1	-	0	SBN 1987
L. salustius	Polygonaceae	2	-	0	Laidlaw 1970, Gibbs 1980
L. feredayi	Polygonaceae	2	-	0	Laidlaw 1970, Gibbs 1980
L. rauparaha	Polygonaceae	2	-	0	Gibbs 1980
L. boldenarum	Polygonaceae	2	-	0	Laidlaw 1970
Heliophorus epicles	Polygonaceae	2	-	0	Johnston & Johnston 1980, Ballmer & Pratt 1988
H. brahma	Polygonaceae	2	-	0	Sevastopulo 1973
H. sena	Polygonaceae	2	-	0	Sevastopulo 1973
Melanolycaena altimontana	Polygonaceae	2	-	0	Sibatani 1974
M. thecloides	Polygonaceae	2	-	0	Sibatani 1974
Theclini:					
Luciiti					
Lucia section					
Lucia limbaria	Oxalidaceae	2	-	3/4(**)	Common & Waterhouse 1981
Paralucia aurifera	Pittosporaceae	3	-	4**	Common & Waterhouse 1981
P. spinifera	Pittosporaceae	2	y	4**	Edwards & Common 1978
P. pyrodiscus	Pittosporaceae	1	-	4**	Common & Waterhouse 1981, Braby 1990
Pseudodipsas eone	Verbenaceae Sapindaceae Dioscoreaceae	5	y	3(**)	Valentine & Johnson 1988
Ps. cephenes	Verbenaceae Sapindaceae Ebenaceae Loranthaceae (lab) Dioscoreaceae (lab?)	5	y	3(**)	Valentine & Johnson 1988
Acrodipsas cuprea	*Crematogaster* brood	-	-	4(*)	Common & Waterhouse 1981
A. myrmecophila	*Iridomyrmex* brood	-	-	4*	Common & Waterhouse 1981
A. illidgei	*Crematogaster* brood	-	-	4*	Samson 1989
Hypochrysops section					
Hypochrysops apollo	Rubiaceae	2	e	4(**)	Common & Waterhouse 1981
H. arronica	Rubiaceae	2?	(e)	4(**)	Sands 1986
H. plotinus	Araliaceae	3	?	4(**)	Sands 1986
H. narcissus	Myrtaceae Rhizophoraceae Combretaceae Loranthaceae Myrsinaceae	5	-	3(**)	Sands 1986, Valentine & Johnson 1988
H. architas	Combretaceae	2	y	3(**)	Sands 1986
H. halyaetus	Mimosaceae Fabaceae	3	?	3(**)	Common & Waterhouse 1981
H. cyane	Myrtaceae	1?	?	3/4(**)	Common & Waterhouse 1981
H. epicurus	Verbenaceae	1?	-	3/4(**)	Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hypochrysops delicia	Mimosaceae Rhamnaceae	4	?	3/4(**)	Common & Waterhouse 1981
H. ignitus	Mimosaceae Fabaceae Caesalpiniaceae Rosaceae Proteaceae, Myrtaceae, Lecythidaceae, Sapindaceae, Rhamnaceae, Santalaceae, Theaceae, Elaeocarpaceae, Epacridaceae, Asteraceae (total 17 families)	5	?	4**	Common & Waterhouse 1981
H. piceatus	Casuarinaceae	1?	?	3(**)	Common & Waterhouse 1981
H. miskini	Myrtaceae Melastomataceae Sapindaceae Euphorbiaceae Myrsinaceae, Verbenaceae, Dioscoreaceae, Smilacaceae	5	?	4(**)	Common & Waterhouse 1981, Sands 1986, Valentine & Johnson 1989
H. digglesii	Loranthaceae	3	-	3(**)	Common & Waterhouse 1981, Sands 1986
H. apelles	Fabaceae Mimosaceae Myrtaceae Barringtoniaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Rhamnaceae, Euphorbiaceae, Verbenaceae	5	?	4**	Common & Waterhouse 1981, Sands 1986, Ballmer & Pratt 1988
H. dicomas	??	?	?	4(**)	Sands 1986
H. byzos	Rhamnaceae	2	?	1/2(**)	Common & Waterhouse 1981
H. geminatus	Sterculiaceae	2	?	(1/2**)	Sands 1986
H. pythias	Sterculiaceae Tiliaceae ??	3?	?	0(?**)	Valentine & Johnson 1988
H. polycletus	Malpighiaceae (ov.)	?	?	4?(**)	Sands 1986
H. theon	Polypodiaceae	1?	e	3/4(**)	Common & Waterhouse 1981
H. dohertyi	Polypodiaceae (ov.)	1?	?	(3**)	Sands 1986
Philiris nitens	Euphorbiaceae	1?	(-)	0	Common & Waterhouse 1981, Ballmer & Pratt 1988
Ph. helena	Euphorbiaceae	2	-	0/1	Parsons 1984
Ph. agatha	Euphorbiaceae	2	-	0/1	Parsons 1984
Ph. innotata	Moraceae	2?	(-)	(0)	Common & Waterhouse 1981
Ph. moira	Moraceae	2	-	0*?	Forbes 1977
Ph. kapaura	Moraceae ?	(2)	(-)	(0)	Parsons 1984
Ph. ziska	Moraceae	1	-	2/3**?	Parsons 1984
Ph. intensa	Urticaceae	1?	-	2*?	Parsons 1984
Ph. fulgens	Lauraceae	2?	-	0	Wood 1984
Ph. diana	Lauraceae	2?	-	0	Wood 1984
Ph. harterti	Lauraceae	2?	-	(0)	Parsons 1984
Ph. violetta	Lauraceae	2?	-	(0)	Parsons 1984
Ph. praeclara	Lauraceae	2?	-	(0)	Parsons 1984
Ogyriti					
Ogyris genoveva	Loranthaceae	3	-	4**	Common & Waterhouse 1981
O. zosine	Loranthaceae	2	-	3**	Common & Waterhouse 1981
O. idmo	Loranthaceae ?	?	?	(3/4**)	Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Ogyris otanes	Santalaceae	2?	-	4**	Common & Waterhouse 1981
O. abrota	Loranthaceae	3	-	3**	Common & Waterhouse 1981
O. olane	Loranthaceae	3	-	2**	Common & Waterhouse 1981
O. barnardi	Loranthaceae	2?	-	3**	Common & Waterhouse 1981
O. ianthis	Loranthaceae	3	-	3**	Common & Waterhouse 1981
O. iphis	Loranthaceae	3	-	3**	Common & Waterhouse 1981
O. aenone	Loranthaceae	3	-	3**	Common & Waterhouse 1981
O. oroetes	Loranthaceae	2?	-	(3**)	Common & Waterhouse 1981
O. amaryllis	Loranthaceae	2	-	3/4**	Common & Waterhouse 1981
Zesiiti					
Zesius chrysomallus	Fabaceae	5	y	4*(*)	Bell 1915, Yates 1932,
	Mimosaceae ?				Hinton 1951
	Combretaceae				
	Anacardiaceae				
	Dioscoreaceae				
	+ *Zesius* larvae/pupae, + *Oecophylla* brood ?				
Jalmenus evagoras	Mimosaceae	2	y	4**	Common & Waterhouse 1981
J. eichhorni	Mimosaceae	2	(y)	3**	Common & Waterhouse 1981
J. ictinus	Mimosaceae	4	(y)	4**	Common & Waterhouse 1981
	Sapindaceae				
J. pseudictinus	Mimosaceae	4	(y)	4**	Common & Waterhouse 1981
	Sapindaceae				
J. daemeli	Mimosaceae	5	y	4**	Common & Waterhouse 1981
	Myrtaceae				
	Sapindaceae				
J. lithochroa	Mimosaceae	1?	y, i	3**	Common & Waterhouse 1981
J. inous	Mimosaceae	1?	(y)	3**	Common & Waterhouse 1981
J. icilius	Mimosaceae	3	(y)	3/4**	Common & Waterhouse 1981
	Caesalpiniaceae				
J. clementi	Mimosaceae	2	(y)	2/3**	Common & Waterhouse 1981
Pseudalmenus chlorinda	Mimosaceae	2	y	3/4**	Common & Waterhouse 1981
Arhopaliti					
Arhopala amphimuta	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. moolaiana	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. zylda	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. bazalus	Fagaceae	3	?	3**	Iwase 1954
A. amantes	Fabaceae ?	4?	?	3**	Viehmeyer 1910b,
	Combretaceae ?				Bell 1915
A. pseudocentaurus	Fagaceae	5	y	4**	Norman 1949,
	Lythraceae				Corbet & Pendlebury 1978,
	Myrtaceae				Kirton & Kirton 1987,
	Combretaceae				Ballmer & Pratt 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Arhopala centaurus	Myrtaceae	5	y	4**	Valentine & Johnson 1988
	Combretaceae				
	Lythraceae				
	Loranthaceae				
A. micale	Lauraceae	5	(y)	3**	Common & Waterhouse 1981
	Lythraceae				
	Myrtaceae				
	Combretaceae				
	Sapindaceae				
	Euphorbiaceae				
A. madytus	Combretaceae	5	(y)	(3**)	Valentine & Johnson 1988
	Sterculiaceae				
	Malvaceae				
	Boraginaceae				
	Verbenaceae				
A. meander	??	?	?	(3**)	Viehmeyer 1910a
A. japonica	Fagaceae	3	?	3*(*)	Iwase 1954
A. rama	Fagaceae	2?	?	(3**)	Sevastopulo 1973
A. ganesa	Fagaceae	3	?	3**	Iwase 1954
A. birmana	Fagaceae	3?	?	(3**)	Uchida 1984
A. (Mahathala)					
ameria	Euphorbiaceae	4	?	(3)**	Uchida 1984
	Boraginaceae				
Thaduka multicaudata	Euphorbiaceae	1?	y	2/3**	Bell 1915, Hinton 1951
Flos apidanus	Myrtaceae	4	?	(3**)	Corbet & Pendlebury 1978
	Lythraceae				
F. areste	??	?	?	(3)**	Ballmer & Pratt 1988
F. fulgida	??	?	?	3**	Ballmer & Pratt in press
Surendra quercetorum	Mimosaceae	3	y	3**	Bell 1915
ssp.? *vivarna*	Mimosaceae	1?	y	3**	Maschwitz et al. 1985b
Thecliti					
Artopoetes pryeri	Oleaceae	3	y, i	(0)	Shirôzu 1961 [62], Shirôzu & Hara 1974
Coreana raphaelis	Oleaceae	2	y, i	(0)	Iwase 1954
Ussuriana michaelis	Oleaceae	2	?	(0)*?	Shin 1970
U. ibara	Oleaceae	2	?	(0*)	Iwase 1954
U. stygiana	Oleaceae	2	?	0(*)	Shirôzu 1961 [62]
Laeosopis roboris	Oleaceae	2	–	(0)*?	Agenjo 1963
Thecla betulae	Rosaceae	4/5?	y	1	Shirôzu 1961 [62],
	Betulaceae (lab ?)			pupa: 3	Emmet & Heath 1990
	Corylaceae (lab ?)				
	Salicaceae ??				
Th. betulina	Rosaceae	2	(y)	(0/1)	Shirôzu 1961 [62]
Shirozua jonasi	Fagaceae	2/4?	?	4	Shirôzu 1961 [62],
	Anacardiaceae ?				Cottrell 1984,
	Lachnidae				Pierce & Elgar 1985
	Coccidae				
	+ *Lasius* regurgitations				

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Antigius attilia	Fagaceae	3	?	(0)	Shirôzu 1961 [62]
A. butleri	Fagaceae	2/3	?	0(*?)	Shirôzu 1961 [62]
Wagimo signata	Fagaceae	2/3	?	(0)	Iwase 1954,
+ ssp. *quercivora*	Fagaceae	2	?	(0)	Shirôzu 1961 [62]
Araragi enthea	Juglandaceae	3/4	y	(0*?)	Iwase 1954,
	Fagaceae (lab?)				Shirôzu 1961 [62]
Chaetoprocta odata	Juglandaceae	2	?	(0)	Sevastopulo 1973
Japonica lutea	Fagaceae	3	?	(0)	Shirôzu 1961 [62]
J. saepestriata	Fagaceae	3	?	(0)	Iwase 1954
Habrodais grunus	Fagaceae	3	y	0	Ballmer & Pratt 1988
Iratsume orsedice	Hamamelidaceae	2	?	(0)	Iwase 1954
Neozephyrus taxila	Betulaceae	2/5	?	(0)	Iwase 1954,
	Fagaceae (lab?)				Shirôzu 1961 [62]
	Rosaceae (?, lab?)				
Chrysozephyrus birupa	Ericaceae	2?	?	(0)	Sevastopulo 1973
Ch. smaragdinus	Rosaceae	5	?	(0)	Shirôzu 1961 [62]
	Fagaceae				
	Corylaceae				
	Ulmaceae (lab?)				
Ch. aurorinus	Fagaceae	2/3	?	(0)	Shirôzu 1961 [62]
Ch. hisamatsusanus	Fagaceae ?	2	?	(0)	Iwase 1954
Ch. ataxus	Fagaceae	2/3	?	(0)	Shirôzu 1961 [62]
Hypaurotis crysalus	Fagaceae	1?	?	0	Scott 1986
Favonius orientalis	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
F. yuasai	Fagaceae	2	y, i	(0)	Iwase 1954
F. ultramarinus	Fagaceae	2/3	i	(0)	Shirôzu 1961 [62]
ssp. *jezoensis*	Fagaceae	2/3	i	(0)	Iwase 1954
ssp. *hayashii*	Fagaceae	2	(i)	(0)	Iwase 1954
F. saphirinus	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
F. cognatus	Fagaceae	2/3	i	(0)	Shirôzu & Hara 1974
F. latifasciatus	Fagaceae	2/3	y	(0)	Shirôzu 1961 [62]
F. fujisanus	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
Quercusia quercus	Fagaceae	2/5?	y, i	0	Shirôzu 1961 [62],
	Myricaceae (lab ?)			pupa: 2	Emmet & Heath 1990
	Oleaceae (lab ?)				
Amblopala avidiena	Mimosaceae	2?	y	(3)**	Uchida 1985
Eumaeini:					
Catapaecilmatiti					
Catapaecilma major	Combretaceae	2?	(y)	3(**)	Corbet & Pendlebury 1978
C. elegans	Combretaceae	2	y	3**	Hinton 1951
Amblypodiiti					
Amblypodia anita	Olacaceae	2?	y	0**	Bell 1915, Hinton 1951
Iraota rochana	Moraceae	2	(y)	(2**)	Corbet & Pendlebury 1978

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iraota timoleon	Moraceae	2	y, f, e	2**	Bell 1915, Corbet & Pendlebury 1978
Myrina silenus	Moraceae	2	y, f, e	3**	Henning 1983a
M. dermaptera	Moraceae	2	-	2**	Clark & Dickson 1971
M. subornata	Moraceae	2	-	(2)**	Hinton 1951
M. sharpei	Moraceae (ov.)	2	?	(2**)	van Someren 1974
M. annettae	Moraceae	2	?	(2**)	Ackery & Rajan 1990
Loxuriti					
Loxura atymnus	Dioscoreaceae Smilacaceae	3	y	3**	Corbet & Pendlebury 1978, pers. obs.
L. cassiopeia	Dioscoreaceae	2	y	(3**)	Pinratana 1981
Yasoda pita	Dioscoreaceae Smilacaceae	3	(y)	(3**)	Corbet & Pendlebury 1978
Eooxylides tharis	Dioscoreaceae Smilacaceae	3	y	3**	Corbet & Pendlebury 1978,
Cheritra freja	Mimosaceae Lauraceae Rubiaceae	5	y	0	Bell 1915, Corbet & Pendlebury 1978, Ballmer & Pratt 1988
Drupadia ravindra	Mimosaceae Caesalpiniaceae Myrtaceae	5	y	3**	Corbet & Pendlebury 1978, pers. obs.
D. theda	Caesalpiniaceae Rubiaceae	4	y, i	3**	Maschwitz et al. 1985b, pers. obs.
Dapidodigma demeter	Mimosaceae	2?	?	?	Ackery & Rajan 1990
Horaga albimacula anyta	Euphorbiaceae	2?	?	?	Uchida 1984
H. onyx	Coriariaceae	1?	?	?	Sevastopulo 1973
Rathinda amor	Myrtaceae Sapindaceae Euphorbiaceae Loranthaceae Styracaceae Rubiaceae	5	i, f	?	Bell 1915, Sevastopulo 1938, 1973
Iolaiti					
Iolaus (Iolaus) bolissus	Loranthaceae	2	?	?	Kielland 1990
I. (Hemiolaus) coeculus	Olacaceae	1?	?	?	Migdoll 1988
I. (Stugeta) bowkeri	Loranthaceae Olacaceae	4	-	0?**	Clark & Dickson 1971, Kielland 1990
I. (S.) marmorea	Olacaceae	2	y	0?	Jackson 1937
I. (S.) mimetica	Olacaceae Loranthaceae (ov)	4	?	?	van Someren 1974, Sevastopulo 1975
I. (S.) carpenteri	Olacaceae Loranthaceae (ov)	4	y, i	?	van Someren 1974, Sevastopulo 1975

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iolaus (Pseudiolaus) poultoni	Loranthaceae	3	y, i	?	van Someren 1974, Kielland 1990
I. (Tanuetheira) timon	Loranthaceae	1?	i	0?	Farquharson 1922
I. (Argiolaus) silas	Loranthaceae	3	(y)	0?**	Clark & Dickson 1971
I. (A.) silarus	Loranthaceae	3	(y)	(0?**)	Henning & Henning 1984, Kielland 1990
I. (A.) crawshayi	Loranthaceae	3	y, i	0?	Jackson 1937, Kielland 1990
I. (A.) lalos	Loranthaceae	2?	?	?	Kielland 1990
I. (A.) stewarti	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Iolaphilus) alcibiades	Loranthaceae	2	i	2?(*?)	Farquharson 1922
I. (I.) julus	Loranthaceae	2	i	2*	Farquharson 1922, Hinton 1951
I. (I.) menas	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (I.) paneperata	Loranthaceae	2	i	0*	Farquharson 1922
I. (I.) trimeni	Loranthaceae	3	-	(0?)**	Henning 1983a
I. (I.) ismenias	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (I.) iturensis	Loranthaceae	2	?	?	Kielland 1990
I. (I.) maritimus	Loranthaceae	3	?	?	Kielland 1990
I. (I.) ndolae	Loranthaceae	3	?	?	Kielland 1990
I. (I.) cottrelli	Loranthaceae (ov.)	2	?	?	Kielland 1990
I. (I.) poecilaon	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Philiolaus) parasilanus	Loranthaceae	2	?	?	van Someren 1974
I. (Ph.) dianae	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Aphniolaus) pallene	Olacaceae Loranthaceae	4	-	?	Sevastopulo 1975, Kielland 1990
I. (Epamera) sidus	Loranthaceae	3	y, i	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) mimosae	Loranthaceae	3	-	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) laon	Loranthaceae	1?	i	0?	Farquharson 1922
I. (E.) farquharsoni	Loranthaceae	1?	i	0?	Farquharson 1922
I. (E.) tajoraca	Loranthaceae	1?	y, i	0?	Jackson 1937, van Someren 1974
I. (E.) aphnaeoides	Loranthaceae	3	?	?	Kielland 1990
+ ssp. *diametra*	Loranthaceae	2?	i	?	Kielland 1990
+ ssp. *nasisii*	Loranthaceae	3	y, i	?	Kielland 1990
I. (E.) australis	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) congdoni	Loranthaceae	2	?	?	Kielland 1990
I. (E.) mursei	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) penningtoni	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) scintillans	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) dubiosa	Loranthaceae	3	?	?	Kielland 1990
I. (E.) pseudopollux	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) arborifera	Loranthaceae (ov)	2?	?	?	van Someren 1974
I. (E.) helenae	Loranthaceae	1?	?	?**	Henning & Henning 1989

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iolaus (Epamera) iasis	Loranthaceae	1?	i	0?	Farquharson 1922, van Someren 1974
I. (E.) mermis	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) violacea	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) aethria	Loranthaceae	2	(i)	0?	Farquharson 1922
I. (E.) bansana	Loranthaceae	1?	y, i	?	Jackson 1937, van Someren 1974
I. (E.) glaucus	Loranthaceae	2/3	i	2(**)	Larsen 1980, Ackery & Rajan 1990
I. (E.) alienus	Loranthaceae	3	-	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) aemulus	Loranthaceae	2	i	?**	Migdoll 1988
I. (E.) obscurus	Loranthaceae	2	(i)	?	Pennington et al. 1978
I. (E.) maesa	Loranthaceae	2	i	3(**)	Farquharson 1922
Pratapa deva	Loranthaceae	2	?	2**	Corbet & Pendlebury 1978
Creon cleobis	Loranthaceae	3	y	2**	Bell 1915, Hinton 1951, Johnston & Johnston 1980
Tajuria cippus	Loranthaceae	3	?	1/2**	Bell 1915, Corbet & Pendlebury 1978
T. melastigma	Loranthaceae	2	?	(2**)	Sevastopulo 1973
T. diaeus	Loranthaceae Verbenaceae ??	2	?	(2**)	Sevastopulo 1973
T. mantra	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
T. deudorix	Loranthaceae	2	?	(2**)	Corbet & Pendlebury 1978
T. dominus	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
T. caerulea	Loranthaceae	2?	?	(2**)	Uchida 1985
Charana mandarinus	Loranthaceae ?	2?	?	(1**)	Toxopeus 1933
Eliotia jalindra	Loranthaceae	2	?	(1**)	Sevastopulo 1973
+ ssp. *indra*	Loranthaceae	2	?	1**	Bell 1915, Hinton 1951
Jacoona anasuja	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
Remelaniti					
Ancema blanka	Loranthaceae	2	?	(2)*	Bell 1915, Hinton 1951
Remelana jangala	Hypericaceae Myrsinaceae Ericaceae	5	?	3*	Johnston & Johnston 1980, Young 1991
Hypolycaeniti					
Hypolycaena erylus	Rubiaceae Lauraceae	4	(y)	4*	Jacobson 1912, Corbet & Pendlebury 1978
H. phorbas	Caesalpiniaceae Myrtaceae Lecythidaceae Rhizophoraceae Combretaceae, Sapindaceae, Loranthaceae, Myrsinaceae, Verbenaceae, Flagellariaceae	5	y, i	4*	Common & Waterhouse 1981, Valentine & Johnson 1988, Moss 1989
H. pachalica	Combretaceae (ov) Cucurbitaceae	4	(i, f)	(3*)	van Someren 1974, Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hypolyc. philippus	Sapindaceae	5	i, f, e	3*	Clark & Dickson 1971,
	Punicaceae				Sevastopulo 1975,
	Olacaceae				Ackery & Rajan 1990
	Loranthaceae				
	Cucurbitaceae, Rubiaceae, Bignoniaceae, Verbenaceae, Fabaceae ?				
H. nigra	??	?	?	3(*)	Hinton 1951
H. danis	Orchidaceae	3	y, i, f	(2*)	Common & Waterhouse 1981
H. (Tatura) lebona	??	?	?	3*(*)	Hinton 1951
H. (Chliaria) kina	Orchidaceae	3	i	(2*)	Corbet & Pendlebury 1978
H. (Ch.) othona	Orchidaceae	3	i, f, e	2**(?)	Bell 1915, Hinton 1951
Leptomyrina hirundo	Crassulaceae	3	e	3*	Migdoll 1988
L. lara	Crassulaceae	4	e	2/3*	Sevastopulo 1975,
	Aizoaceae				Migdoll 1988
L. henningi	Crassulaceae	3	(e)	(2*)	Pennington et al. 1978
L. gorgias	Crassulaceae	4	e	2/3*	Migdoll 1988,
	Aizoaceae				Kielland 1990
Deudorigiti					
Deudorix (Virachola)					
diocles	Caesalpiniaceae	5	i, f, e	2/3*	Migdoll 1988
	Mimosaceae				
	Fabaceae				
	Rosaceae				
	Proteaceae, Myrtaceae, Combretaceae				
D. lorisona	Rubiaceae	2?	f, e	?(*)	Kielland 1990
D. vansomereni	Connaraceae	1?	f, e	?(*)	van Someren 1974
D. dariaves	Sapindaceae	5	i, f, e	?(*)	Sevastopulo 1975,
	Caesalpiniaceae				Migdoll 1988
	Rubiaceae				
D. dinomenes	Sapindaceae	1?	f, e	?(*)	Sevastopulo 1975
D. odana	Fabaceae	3	i, f, e	?(*)	Jackson 1947,
	Caesalpiniaceae				Sevastopulo 1975
D. dinochares	Mimosaceae	5	i, f, e	2/3*(*?)	Clark & Dickson 1971
	Fabaceae				
	Rosaceae				
	Proteaceae				
	Myrtaceae, Combretaceae, Olacaceae, Rubiaceae				
D. antalus	Mimosaceae	5	i, f, e	3*(*?)	Jackson 1937,
	Fabaceae				Clark & Dickson 1971,
	Caesalpiniaceae				Sevastopulo 1975,
	Rosaceae				Ackery & Rajan 1990
	Myrtaceae, Combretaceae, Sapindaceae, Olacaceae, Apiaceae, Solanaceae, Aitoniaceae etc.				
D. ecaudata	Mimosaceae	2?	e (galls)	3(*)	van Someren 1974
D. suk	Mimosaceae	2?	e (galls)	3(*)	van Someren 1974
D. vansoni	Mimosaceae	2?	e (galls)	(3*)	Pennington et al. 1978
D. penningtoni	Mimosaceae	2?	e (galls)	(3*)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Deudorix isocrates	Fabaceae	5	i, f, e	1(*)T	Bell 1920, Hinton 1951
	Rosaceae				
	Lythraceae				
	Myrtaceae				
	Punicaceae, Rubiaceae, Loganiaceae				
D. perse	Punicaceae	5	i, f, e	1T	Bell 1920, Hinton 1951
	Myrtaceae				
	Rubiaceae				
D. livia	Fabaceae	5	i, f, e	2/3*	Hinton 1951,
	Mimosaceae				Awadallah et al. 1971,
	Caesalpiniaceae				Larsen 1980
	Rosaceae				
	Punicaceae, Myrtaceae, Solanaceae, Alliaceae, Arecaceae				
D. democles	Loganiaceae	2?	f, e	?	Common & Waterhouse 1981
D. smilis	Loganiaceae	2?	f, e	?	Common & Waterhouse 1981
D. jacksoni	Loranthaceae	1?	y	(0)**(?)	Jackson 1937
D. (Pilodeudorix)					
diyllus	Fabaceae	1?	i, f	3*(*?)	Farquharson 1922
D. camerona	Fabaceae	1?	i, f	2**	Jackson 1947
D. (Hypokopelates)					
obscura	??	?	?	3(*?)	Hinton 1951
D. (Deudorix)					
epijarbas	Punicaceae	5	i, f, e	?*	Hinton 1951,
	Proteaceae				Common & Waterhouse 1981,
	Sapindaceae				Ballmer & Pratt 1988
	Hippocastanaceae				
	Connaraceae, Arecaceae, Rosaceae (lab)				
D. epirus	Sapindaceae	2?	f, e	?	Common & Waterhouse 1981
Artipe eryx	Rubiaceae	1?	i, f, e	0	Shirôzu & Hara 1974,
					Johnston & Johnston 1980
Sinthusa chandrana	Rosaceae	2?	y, (e?)	?	Johnston & Johnston 1980
Bindahara phocides	Hippocrateaceae	5	f, e	0	Storey & Lambkin 1983
+ ssp. *sugriva*	Rhamnaceae		i, f, e	0/1*	Bell 1915, Hinton 1951
	Celastraceae				
Rapala pheretima	Caesalpiniaceae	4	y, i	3(**)	Norman 1976
	Lythraceae				
R. dieneces	Myrtaceae	3	(i, f)	(2**)	Corbet & Pendlebury 1978
R. iarbus	Fabaceae	5	y, i	3**	Sevastopulo 1973,
	Melastomataceae				Corbet & Pendlebury 1978,
	Sapindaceae				pers. obs.
	Rhamnaceae				
R. manea	Mimosaceae	5	i, f	3**	Hinton 1951,
	Caesalpiniaceae				Sevastopulo 1973,
	Fabaceae				Seki et al. 1991
	Rosaceae				
	Sapindaceae, Combretaceae, Theaceae, Caprifoliaceae, Verbenaceae				
R. nissa rectivitta	??	?	?	(2)**	Sevastopulo 1941

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Rapala varuna	Fabaceae	5	y, i, f, e	(1/2**)	Jayaraj et al. 1961,
	Mimosaceae				Common & Waterhouse 1981,
	Myrtaceae				Lambkin 1983,
	Sapindaceae				Valentine & Johnson 1988
	Rhamnaceae				
	Verbenaceae				
R. rhoecus (?)	Melastomataceae	4	(y, i)	(2**)	Sevastopulo 1973
[as *sphinx*]	Elaeagnaceae				
R. selira	Fabaceae	2?	(y, i)	(2**)	Sevastopulo 1973
R. arata	Fabaceae	5	i, f	3**	Iwase 1954, Shirôzu
	Saxifragaceae				& Hara 1974
	Rosaceae				
	Ericaceae				
	Symplocaceae				
	Rhamnaceae				
R. caerulea	Fabaceae	3?	(i?)	(2**)	Uchida 1985
R. takasagonis	Piperaceae	2?	(i?)	(2**)	Uchida 1985
Capys alphaeus	Proteaceae	2	i, f, e	(0)*	Clark & Dickson 1971
ssp.? *brunneus*	Proteaceae	2	i, e	(0*)	Kielland 1990
C. penningtoni	Proteaceae	2	i, f	(0*)	Migdoll 1988
C. disjunctus	Proteaceae	2	i, f, e	(0)*	Clark & Dickson 1971
ssp.? *connexivus*	Proteaceae	2	i, e	(0*)	Kielland 1990
C. catharus	Proteaceae	2	i, e	(0)*	Jackson 1947
Tomares ballus	Fabaceae	3	(i, f)	2**	Martín 1982, Jordano
					et al. 1990a & b
T. romanovi	Fabaceae	2?	i, f	3(**)	Weidenhoffer & Vanek 1977
T. callimachus	Fabaceae	1?	(i, f)	3**	Malicky 1969b,
					Weidenhoffer & Vanek 1977
T. nogelii	Fabaceae	2	i, f	3(**)	Hesselbarth &
					Schurian 1985
T. nesimachus	Fabaceae	1	(i)	(3**)	Larsen & Nakamura 1983
T. mauritanicus	Fabaceae	1?	y, i	(3)**	Malicky 1969b,
					Courtney 1983
Eumaeiti:					
Eumaeus atala	Cycadaceae	3/4?	y	0	Ehrlich & Raven 1964,
	Euphorbiaceae ?				Scott 1986
Eu. minijas	Cycadaceae	3	y	0	Scott 1986
Eu. childrenae	Cycadaceae	3/4?	y	0	Ross 1964b,
	Amaryllidaceae ?				Ehrlich & Raven 1964
	Agavaceae ?				
Eu. godartii	Cycadaceae	2	(y)	0	DeVries, pers. comm.
Eu. toxea	Cycadaceae	3	y	0	Ross 1964b
[as *minyas*]					
Micandra platypera	Fabaceae	2	y	?	DeVries, pers. comm.
Evenus regalis	Sapotaceae	3	y, i, f	?	Zikan 1956, Kendall 1975
E. coronata	Sapotaceae	2	y	?	Schultze-Rhonhof 1938
E. latreillii	Sapotaceae	2	y	?	Hoffmann 1937b

Table 17 (continued)

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Allosmaitia coelebs	Malpighiaceae	2?	y, e	?	Riley 1975
Theritas triquetra	Melastomataceae, Euphorbiaceae, Ulmaceae	5	y	?	Jörgensen 1935, Hoffmann 1937a
Pseudolycaena damo	Fabaceae, Rosaceae, Sapindaceae, Euphorbiaceae	5	y, i	3*	Kendall 1975, Robbins & Aiello 1982, DeVries 1990a
Ps. marsyas	Rosaceae, Myrtaceae, Combretaceae, Anacardiaceae, Sapindaceae, Celastraceae, Sterculiaceae, Sapotaceae, Ulmaceae	5	y, i	(3*?)	Kirkpatrick 1953, Zikan 1956, d'Araujo e Silva et al. 1967/68
Ps. nellyae	Fabaceae, Annonaceae, Meliaceae, Malpighiaceae, Sapotaceae	5	(y)	?	Lamas 1975
Arcas ducalis	Annonaceae	2?	?	0	Zikan 1956
Atlides halesus	Loranthaceae	2	i	0*	Ballmer & Pratt 1988
A. near *cosa* [as *atys*]	Loranthaceae	1?	?	(0*)	Zikan 1956
Arawacus lincoides [as *aetolus*]	Solanaceae	3	(-)	3*	Robbins & Aiello 1982, Robbins, in press
A. separata [as *aetolus*]	Solanaceae	2?	(-)	(3*)	Robbins & Aiello 1982
A. meliboeus	Solanaceae	2	(-)	(3*)	Hoffmann 1937a
A. jada	Solanaceae	2	-	(3*)	Scott 1986
A. ellida	Solanaceae	2?	-	(3*)	Robbins 1991
Thereus pedusa	Loranthaceae	1?	y, i	3*	DeVries, pers. comm.
Th. near *enenia*	Malpighiaceae, Chrysobalanaceae, Malvaceae (lab)	5	y, i	3*	Robbins & Aiello 1982, DeVries 1990a
Rekoa palegon	Euphorbiaceae, Ulmaceae, Solanaceae, Boraginaceae, Verbenaceae, Asteraceae	5	y, i, e	3*	Malicky 1969b, DeVries 1990a, Robbins 1991
R. marius	Fabaceae, Caesalpiniaceae, Polygonaceae, Myrtaceae, Melastomataceae, Combretaceae, Sapindaceae, Malpighiaceae, Ochnaceae, Apocynaceae, Boraginaceae, Bignoniaceae, Verbenaceae	5	y, i, f, e	0?(*)	Robbins & Aiello 1982, Robbins 1991
R. stagira	Fabaceae, Malpighiaceae	4	y	?	Robbins 1991
R. zebina	Fabaceae	3?	i	?	Robbins 1991
Contrafacia muattina	Fabaceae	2?	y	0	Hoffmann 1932

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Chlorostrymon simaethis	Sapindaceae	5	f, e	2/3(*)	Zikan 1956, Scott 1986, DeVries 1990a & pers comm.
	Asteraceae				
	Fumariaceae ?				
	Solanaceae ?				
	Scrophulariaceae ?				
Ch. maesites	Mimosaceae (lab)	3	i, f	(2*)	Scott 1986
Harkenclenus titus	Rosaceae	3/4?	y, i, f	2*	Harvey & Webb 1980, Klassen et al. 1989
	Fagaceae ?				
Satyrium (Fixsenia) pruni	Rosaceae	2	i	0	Kitching & Luke 1985
S. (F.) watarii	Rosaceae	2?	?	(0)	Uchida 1985
S. (F.) favonius	Fagaceae	2	y, i	(0)	Scott 1986
S. (F.) polingi	Fagaceae	2	(y, i)	(0)	Scott 1986
S. formosana	Sapindaceae	2?	?	?(*)	Uchida 1985
S. w-album	Ulmaceae	5	i, f	2*	SBN 1987
	Fagaceae				
	Rosaceae				
	Rhamnaceae				
	Tiliaceae				
S. spini	Rhamnaceae	2	-	2*	SBN 1987
S. jebelia	Rhamnaceae	1	(-)	(2*)	Larsen 1990
S. merus	Rhamnaceae	2	?	?*	Iwase 1954
S. iyonis	Rhamnaceae	2	?	?*	Taketsuka & Akizawa 1978
S. saepium	Rhamnaceae	2?	?	?*	Ballmer & Pratt 1988
S. californica	Fagaceae	5	-	?*	Ballmer & Pratt 1988
	Rosaceae				
	Rhamnaceae				
	Salicaceae				
S. acadica	Salicaceae	2	-	?*	Scott 1986
S. sylvinus	Salicaceae	2	-	?*	Ballmer & Pratt 1988
S. liparops	Rosaceae	5	y, i, f	?(*)	Scott 1986
	Fagaceae				
	Betulaceae				
	Juglandaceae				
	Salicaceae				
	Ericaceae				
	Oleaceae				
S. kingi	Symplocaceae	4	y	?(*)	Scott 1986
	Ericaceae (lab)				
S. caryaevorus	Fagaceae	5	-	?(*)	Scott 1986
	Juglandaceae				
	Oleaceae				
	Rosaceae ?				
S. calanus	Fagaceae	5	y, i	?(*)	Scott 1986
	Juglandaceae				
	Rosaceae				
	Aceraceae				
	Oleaceae				
S. auretorum	Fagaceae	2	-	?*	Ballmer & Pratt 1988
S. edwardsii	Fagaceae	2	y	3/4*	Webster & Nielsen 1984

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Satyrium ilicis	Fagaceae	2	y	2*	SBN 1987
S. esculi	Fagaceae	2	(y)	3*	Martín & Gurrea 1983, Devarenne 1990
S. myrtale	Rosaceae	2/3	?	(0*)	Nakamura 1976
S. acaciae	Rosaceae	3	i	0*	SBN 1987
+ ssp.? *persica*	Rosaceae ?	2?	?	(0)	Larsen 1974
S. marcida	Rosaceae ?	2?	?	?	van Oorschot et al. 1985
S. behrii	Rosaceae	2	-	?*	Ballmer & Pratt 1988
S. tetra	Rosaceae	2?	-	?*	Ballmer & Pratt 1988
S. ledereri	Fabaceae ?	?	?	?(*)	Olivier 1989
S. hyrcanica	Fabaceae ?	?	?	?(*)	Olivier 1989
S. rhymnus	Fabaceae	?	?	(3*)	Zhdanko 1983
S. tengstroemi	Fabaceae	2?	?	3*	Viehmeyer 1907, Eckweiler, pers. comm.
S. sinensis	Fabaceae ?	2?	?	(3*)	Eckweiler, pers. comm.
S. fuliginosum	Fabaceae	2	?	3*	Ballmer & Pratt 1988
Callophrys rubi	Fabaceae Rosaceae Rhamnaceae Cistaceae Cornaceae, Ericaceae, Caprifoliaceae, + lab: Ranunculaceae, Polygonaceae, Hippocastanaceae, Oxalidaceae, Geraniaceae, Tiliaceae, Asteraceae, Alliaceae	5	y, i, f	0/1*	SBN 1987, Fiedler 1990d
C. avis	Ericaceae	3	i, f	(0*)	Dujardin 1972, Martín 1982, Devarenne 1990
C. affinis	Polygonaceae	2/3	i, f	(0*)	Scott 1986
C. perplexa	Fabaceae Polygonaceae	4	i, f	0*	Ballmer & Pratt 1988
C. dumetorum	Polygonaceae Fabaceae	4	i, f	0*	Ballmer & Pratt 1988
C. sheridanii	Polygonaceae	2	-	(0*)	Scott 1986
C. lemberti	Polygonaceae Fabaceae	4	-	0*	Ballmer & Pratt 1988
C. comstocki	Polygonaceae	1?	-	0*	Ballmer & Pratt 1988
C. (Incisalia) eryphon	Pinaceae Cupressaceae	3	y, i. e	0*	Ballmer & Pratt 1988
C. (I.) niphon	Pinaceae Cupressaceae ?	3	y	(0*)	Scott 1986
C. (I.) lanoraieensis	Pinaceae	2	y	(0*)	Scott 1986
C. (Sandia) irus	Fabaceae	3	i, f	(0*)	Scott 1986
C. (S.) henrici	Fabaceae Rosaceae Ebenaceae Aquifoliaceae Ericaceae, Caprifoliaceae, Cyrillaceae ?	5	y, i, f, e	(0*)	Scott 1986
C. (S.) polios	Ericaceae	3	y, i	(0*)	Scott 1986

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Callophrys (Sandia) augustinus	Rosaceae Polygonaceae Rhamnaceae Ericaceae Hydrophyllaceae, Convolvulaceae, Liliaceae	5	i, f, e	0*	Ballmer & Pratt 1988, Klassen et al. 1989
C. (S.) fotis	Rosaceae	1?	i, f	0*	Ballmer & Pratt 1988
C. (S.) mossii	Crassulaceae	2	i, e	0*	Emmel & Ferris 1972
C. (S.) xami	Crassulaceae	3	e	2(*)	Ziegler & Escalante 1964, Scott 1986
C. (S.) mcfarlandi	Agavaceae	2	i, f	2*	Scott 1986
C. (Mitoura) nelsoni	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) siva	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) loki	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) thornei	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) cedrosensis	Cupressaceae ?	1?	?	(0*)	Brown & Faulkner 1989
C. (M.) gryneus	Cupressaceae	2	y, i	0*	Scott 1986
C. (M.) hesseli	Cupressaceae	1?	y	(0*)	Scott 1986
C. (M.) johnsoni	Loranthaceae	2	-	0*	Ballmer & Pratt 1988
C. (M.) spinetorum	Loranthaceae	2	-	0*	Ballmer & Pratt 1988
C. (Ahlbergia) ferrea	Caprifoliaceae Ericaceae Rosaceae	5	i, f	0	Iwase 1954, Shirôzu & Hara 1974
C. (A.) haradai	Rutaceae	1?	f	0	Igarashi 1973
C. (Cyanophrys) goodsoni	Phytolaccaceae	1?	i, f	(0*)	Scott 1986
C. (Cy.) miserabilis	Fabaceae Caesalpiniaceae Asteraceae	5	i	(0*)	Scott 1986, Robbins, pers. comm.
C. (Cy.) amyntor	Ulmaceae Verbenaceae	4	y, i	(0*)	Kendall 1975, Robbins, pers. comm.
C. (Cy.) herodotus	Anacardiaceae Caprifoliaceae Boraginaceae Verbenaceae Asteraceae	5	i, f	(0*)	Robbins & Aiello 1982, Scott 1986
C. (Cy.) longula	Verbenaceae Asteraceae	4	i	(0*)	DeVries, pers. comm.
C. (Cy.) near *pseudolongula* [as *longula*]	Fabaceae Malvaceae Sterculiaceae Asteraceae (lab)	5	(i)	(0*)	Zikan 1956, Biezanko et al. 1974
C. (Cy.) remus	Fabaceae	2?	(i)	(0*)	Biezanko et al. 1966
Chalybs janias	Fabaceae	1?	-	?	DeVries, pers. comm.
Ch. hassan [as *janias*]	Fabaceae	2?	?	?	Hoffmann 1932
Michaelus vibidia	Bignoniaceae	?	i	?	Robbins & Aiello 1982
M. jebus	Fabaceae Mimosaceae	3	i, f	?	d'Araujo e Silva et al. 1967/68

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Oenomaus ortygnus	Annonaceae	2	i, f, e	2*	Hinton 1951, Kendall 1975
Olynthus narbal	Lecythidaceae	1?	i, e	3(*)	DeVries, pers. comm.
O. hypsea	Lecythidaceae	1?	i	(2*)	Nicolay 1982
Parrhasius m-album	Fagaceae Tiliaceae	4	?	0?	Scott 1986
P. polibetes	Euphorbiaceae Fabaceae	4	i	0?	Zikan 1956
P. selika	Fabaceae	1?	i	?	d'Araujo e Silva et al. 1967/68
Panthiades bitias	Mimosaceae Fabaceae Chrysobalanaceae Combretaceae Simaroubaceae Fagaceae, Euphorbiaceae, Sterculiaceae	5	y, i	3(*)	Kirkpatrick 1953, Callaghan 1982, DeVries, pers. comm.
P. hebraeus [as *cimelius*]	Fabaceae Rosaceae	4	(i)	(3*)	d'Araujo e Silva et al. 1967/68
Strymon melinus	Fabaceae Polygonaceae Cactaceae Fagaceae, Myricaceae, Juglandaceae, Cannabaceae, Moraceae, Crassulaceae, Rosaceae, Rutaceae, Zygophyllaceae, Rhamnaceae, Euphorbiaceae, Hypericaceae, Malvaceae, Ericaceae, Apocynaceae, Asclepiadaceae, Boraginaceae, Loasaceae, Scrophulariaceae, Bignoniaceae, Verbenaceae, Lamiaceae, Asteraceae, Liliaceae, Agavaceae, Poaceae, Arecaceae, Pinaceae (total 32 families)	5	y, i, f, e	?*(rud.)	Scott 1986, Ballmer & Pratt 1988
S. mulucha	Fabaceae Melastomataceae Malvaceae Bignoniaceae Amaryllidaceae Orchidaceae	5	i, f	?	d'Araujo e Silva et al. 1967/68
S. avalona	Fabaceae Polygonaceae	4	y, i	?*	Ballmer & Pratt 1988
S. oribata [as *arenicola*]	Fabaceae	1?	f	?	Jörgensen 1934
S. bebrycia	Fabaceae Sapindaceae	4	f, e	?(*)	Scott 1986, Robbins, pers. comm.
S. istapa [as *columella*]	Malvaceae	3/4?	i	?*	Ballmer & Pratt 1988
S. yojoa	Fabaceae Crassulaceae Gesneriaceae Begoniaceae Malvaceae, Alstroemeriaceae, Orchidaceae	5	i, f, e	0/2?*	Kendall 1975 Robbins & Aiello 1982, DeVries, pers. comm.
S. rufofusca	Malvaceae	3	y, i	?(*)	Kendall 1975
S. albata	Malvaceae Flacourtiaceae	4	y, i	?(*)	Kendall 1975, Robbins, pers. comm.

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Strymon martialis	Ulmaceae	5	y, i, f	?(*)	Scott 1986
	Simaroubaceae				
S. acis	Euphorbiaceae	2	i, f	?*(rud.)	Scott 1986
S. alea	Euphorbiaceae	1?	i, f	?(*)	Scott 1986
S. bazochii	Verbenaceae	4	i, f	?(*)	Scott 1986
	Lamiaceae				
S. gabatha	Bromeliaceae	2	i, f, e	?	DeVries, pers. comm.
S. legota	Bromeliaceae	3	f	?	Fonesca 1934
S. oreala	Bromeliaceae	2	f, e	3(*)	Zikan 1956
S. ziba	Bromeliaceae	5	i, f, e	0?*	Robbins & Aiello 1982,
[as *basilides*]	Haemodoraceae				Robbins, pers. comm.
	Musaceae				
	Strelitziaceae				
Electrostrymon					
angelia	Anacardiaceae	1?	y	?	Scott 1986
E. mathewi	Bignoniaceae	3	i	0?	Robbins & Aiello 1982
Calycopis cecrops	Anacardiaceae	5	i	(0)	Scott 1986
	Myricaceae				
	Euphorbiaceae				
C. isobeon	Euphorbiaceae	5	i, f	(0)	Scott 1986,
ssp. of *cecrops*?	Boraginaceae				Robbins, pers. comm.
	Sapotaceae				
	detritus				
C. chacona	Ulmaceae	1?	?	?	Biezanko et al. 1966
ssp. of *cecrops*?					
C. beon	??	?	(i, f)	0	Malicky 1969b
Symbiopsis tanais	Fabaceae	2?	y	0	DeVries, pers. comm.
Tmolus echion	Fabaceae	5	i, f	3*	Ehrlich & Raven 1964,
	Combretaceae				Robbins & Aiello 1982
	Simaroubaceae				
	Anacardiaceae				
	Malpighiaceae, Solanaceae, Boraginaceae, Acanthaceae,				
	Gesneriaceae, Verbenaceae, Lamiaceae, Bromeliaceae				
T. mutina	Lecythidaceae	1?	i	(3*)	DeVries, pers. comm.
Ministrymon leda	Fabaceae	2	i	?*	Ballmer & Pratt 1988
M. clytie	Fabaceae	2	(i)	?(*)	Scott 1986
M. azia	Mimosaceae	3/4?	i	(3*)	Scott 1986,
	Fabaceae				Robbins, pers. comm.
	Malvaceae ?				
Phaeostrymon					
alcestis	Sapindaceae	1?	y	?	Scott 1986
Hypostrymon critola	Celastraceae	1?	?	?	Scott 1986
Erora laeta	Fagaceae	5	f	0	Klots & dos Passos 1981,
	Betulaceae				Scott 1986
	Corylaceae				
	Salicaceae (lab)				
	Rhamnaceae ?				
E. quaderna	Fagaceae	2	f	0	Klots & dos Passos 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iaspis castitas [as *talyra*]	Sterculiaceae	1?	y	3(*)	Kirkpatrick 1953
Ipidecla miranda	Anacardiaceae	1?	?	?	Kaye 1940
"Thecla" phydela	Asteraceae	2	y	0	Zikan 1956
"Th." hesperitis	Combretaceae Bignoniaceae Bromeliaceae	5	i, f	0?	Robbins & Aiello 1982, Robbins, pers. comm.
"Th." hemon	Fabaceae Sterculiaceae	4	y	0?	Robbins & Aiello 1982
"Th." thyrea	??	?	?	0?	Zikan 1956
"Th." hisbon	Fabaceae Lecythidaceae	4	i	0	DeVries, pers. comm.
"Th." lisus	Fabaceae Chrysobalanaceae Meliaceae Sterculiaceae	5	?	0	Kirkpatrick 1953, Zikan 1956
"Th." umbratus	Sapotaceae	3	y	?	Kendall 1975,
"Th." mycon	Fabaceae Sapindaceae	4	y	?	Muyshondt 1974
"Th." keila	Fabaceae	1?	y, i	?	DeVries, pers. comm.
"Th." tympania	Sterculiaceae Melastomataceae	4	y, f	3(*)	Kirkpatrick 1953
"Th." syedra	Sapindaceae	1?	?	?	Matta 1929
"Th." emessa	Malpighiaceae	1?	y	3(*)	DeVries, pers. comm.
"Th." azaria	Begoniaceae	2	i	0	Zikan 1956
Polyommatini:					
Candaliditi					
Candalides gilberti	Loranthaceae ?	?	?	(2**)	Common & Waterhouse 1981
C. margarita	Loranthaceae Sapindaceae	4	y, i	2**	Common & Waterhouse 1981
C. helenita	Lauraceae Euphorbiaceae Sterculiaceae	5	(y, i)	(2**)	Common & Waterhouse 1981, Valentine & Johnson 1988
C. absimilis	Fabaceae Caesalpiniaceae Proteaceae Sapindaceae Sterculiaceae Flagellariaceae	5	y, i	(2**)	Common & Waterhouse 1981
C. consimilis	Cunoniaceae Sapindaceae Araliaceae	5	y, i	(2**)	Common & Waterhouse 1981
C. cyprotus	Fabaceae Proteaceae	4	(y, i)	(2)**	Common & Waterhouse 1981, Atkins & Heinrich 1987
C. erinus	Lauraceae	2?	?	2/3**	Common & Waterhouse 1981
C. geminus	Lauraceae Cassythaceae	3	i	(2/3)**	Edwards 1980, Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Candalides acastus	Lauraceae	2?	i	(2/3**)	Common & Waterhouse 1981
C. hyacinthinus	Lauraceae	2	y, i	(2/3**)	Common & Waterhouse 1981
C. xanthospilos	Thymelaeaceae	2	?	3**	Common & Waterhouse 1981
C. heathi	Thymelaeaceae Scrophulariaceae Plantaginaceae Myoporaceae Lamiaceae	5	?	2**	Common & Waterhouse 1981
C. (Adaluma) urumelia	Rutaceae	2	-	3**	Edwards 1980
C. (Nesolycaena) alboséricea	Rutaceae	2	i	0(**?)	Common & Waterhouse 1981
Lycaenesthiti					
Anthene emolus	Caesalpiniaceae Mimosaceae Fabaceae Combretaceae Meliaceae, Sapindaceae, Verbenaceae ?	5	y	4**	Corbet & Pendlebury 1978, Fiedler & Maschwitz 1989b
A. seltuttus	Caesalpiniaceae Fabaceae Lythraceae Myrtaceae Sapindaceae Sterculiaceae	5	y	4**	Common & Waterhouse 1981, Valentine & Johnson 1988
A. lycaenina	Mimosaceae Anacardiaceae	4	y, f	2/3**	Bell 1915, Hinton 1951
A. lycaenoides	Caesalpiniaceae Fabaceae Mimosaceae Sapindaceae Verbenaceae	5	(y)	4**	Common & Waterhouse 1981, Valentine & Johnson 1988
A. ligures	Ulmaceae	2	?	0?	Jackson 1937
A. definita	Mimosaceae Caesalpiniaceae Fabaceae Myricaceae Crassulaceae, Rosaceae, Anacardiaceae, Sapindaceae, Melianthaceae, Poaceae ??	5	y, i, f	2**	Clark & Dickson 1971
A. uzungwae	Escalloniaceae	1?	?	(2**)	Kielland 1990
A. lemnos	Euphorbiaceae	2	-	(2)**	Clark & Dickson 1971
A. indefinita	Euphorbiaceae Rubiaceae	4	y	(2**)	van Someren 1974, Sevastopulo 1975
A. pitmani	Mimosaceae	3	y	3**	Jackson 1937, Sevastopulo 1975
A. lunulata	Mimosaceae Caesalpiniaceae Combretaceae	5	y	3**	Hinton 1951, Kielland 1990
A. amarah	Mimosaceae	3	y	3**	Clark & Dickson 1971, Milton 1990

Table 17 (continued)

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Anthene larydas	Mimosaceae Caesalpiniaceae Hypericaceae ?	3	y	3**	Clark & Dickson 1971, Sevastopulo 1975, Ackery & Rajan 1990
A. princeps	Mimosaceae	3	y	0?	Jackson 1937
A. butleri	Crassulaceae	3	y, i, f, e	(2)**	Clark & Dickson 1971, van Someren 1974
A. talboti	Mimosaceae	2	y, i	(2)**	Clark & Dickson 1971
A. otacilia	Mimosaceae	3	y	3**	Clark & Dickson 1971, Kielland 1990
A. hodsoni	Mimosaceae	2?	y, e (galls)	3(**)	van Someren 1974
A. lysicles	Mimosaceae	2?	(y)	(3**)	Ackery & Rajan 1990
A. levis	*Crematogaster* regurgitations ?	-	?	4**	Jackson 1937, Hinton 1951, Ackery & Rajan 1990
A. crawshayi	Mimosaceae Caesalpiniaceae	3	y	3**	Jackson 1947, Hinton 1951
A. liodes	Myricaceae Combretaceae Anacardiaceae Sapindaceae	5	?	3**	Hinton 1951, Sevastopulo 1975
A. ? alberta	??	?	?	3/4(**?)	Ackery & Rajan 1990
A. sylvanus	??	?	?	3**	Hinton 1951
A. lachares	??	?	?	3**	Hinton 1951
A. flavomaculatus	??	?	?	3*(*)	Hinton 1951
A. rubricinctus	Fabaceae	1?	i	3(**)	Farquharson 1922
A. (Cupidesthes) wilsoni	Mimosaceae ?	3?	?	4	Jackson 1937
Triclema lamias	Sapotaceae ? Coccidae ?	?	y	(4*)*	Jackson 1947, Hinton 1951
T. ituriensis	Loranthaceae	2?	?	(3**)	Sevastopulo 1975
T. lucretilis	??	?	y	3(*)	Hinton 1951
T. nigeriae	Mimosaceae	2	y, e	4**	Jackson 1937, Hinton 1951
Neurypexina lyzianus	??	?	?	3(**)	Ackery & Rajan 1990
Niphanditi					
Niphanda fusca	Fagaceae + *Camponotus* regurgitations	2	?	4**	Pierce & Elgar 1985, Hama et al. 1989
Polyommatiti					
Cupidopsis section					
Cupidopsis cissus	Fabaceae	3	i, f, e	2/3**	Clark & Dickson 1971
C. iobates	Fabaceae	3	i, f	(2)**	Clark & Dickson 1971
Nacaduba section					
Petrelaea sichela	Fabaceae ?	?	?	?	Clark & Dickson 1971
Nacaduba sinhala	Sapotaceae	2?	i	2**	Bell 1915, Hinton 1951, Sevastopulo 1973
N. pactolus	Mimosaceae	2	y	2**	Bean 1964
N. beroe	Mimosaceae	2	y	(2**)	Bean 1964

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Nacaduba berenice	Proteaceae Sapindaceae Sterculiaceae	5	y, i	3**	Common & Waterhouse 1981
ssp. *plumbeomicans*	Mimosaceae	3?	y, i	2**	Hinton 1951
N. kurava	Sapindaceae Myrsinaceae	5	y, i	(2**)	Common & Waterhouse 1981, Valentine & Johnson 1988
ssp. *perusia*	Dipterocarpaceae	2?	(y)	(2**)	Sevastopulo 1973
N. normani	Fabaceae Sapindaceae Sterculiaceae	5	y	3(**)	Pan & Morishita 1990
N. biocellata	Mimosaceae	2	y, i	3**	Common & Waterhouse 1981
Prosotas dubiosa	Mimosaceae Proteaceae Sapindaceae	5	y, i	2/3**	Common & Waterhouse 1981, Cassidy 1990
P. felderi	Mimosaceae Proteaceae Sapindaceae	5	y, i	(2**)	Common & Waterhouse 1981, Hawkeswood 1988
P. nora	Mimosaceae Fabaceae	3	i	2**	Bell 1915, Hinton 1951, Larsen 1987, Bean 1988
Catopyrops florinda	Caesalpiniaceae Ulmaceae	4	?	3**	Common & Waterhouse 1981
Erysichton lineata	Proteaceae Sapindaceae Boraginaceae	5	i	(3)**	Common & Waterhouse 1981, Ballmer & Pratt 1988
E. palmyra	Loranthaceae	1	i	(3**)	Common & Waterhouse 1981
Neolucia agricola	Fabaceae	3	i, f, e	(0)	Common & Waterhouse 1981
N. hobartensis	Epacridaceae	2	y, i	0(*?)	Common & Waterhouse 1981
N. mathewi	Fabaceae Epacridaceae	4	y, i	(0)	Common & Waterhouse 1981
Theclinesthes onycha	Cycadaceae	3	y	2/3**	Common & Waterhouse 1981
Th. miskini	Mimosaceae Fabaceae Myrtaceae Sapindaceae	5	y	3**	Common & Waterhouse 1981
Th. scintillata	Mimosaceae Proteaceae Sapindaceae	5	i, f	(3**)	Common & Waterhouse 1981
Th. albocincta	Euphorbiaceae	2	y, i, f	3**	Grund & Sibatani 1975
Th. hesperia	Euphorbiaceae	2	(y, i)	(3**)	Common & Waterhouse 1981
Th. serpentata	Chenopodiaceae	3	?	(2/3**)	Common & Waterhouse 1981
Th. sulpitius	Chenopodiaceae	3	?	2/3**	Samson 1987
Danis danis	Rhamnaceae	1?	-	(3*)	Common & Waterhouse 1981
D. hymetus	Rhamnaceae	1?	-	(3)*	Common & Waterhouse 1981, Ballmer & Pratt 1988
D. cyanea	Mimosaceae	2	?	3*	Common & Waterhouse 1981
D. schaeffera	Connaraceae	1?	?	(3*)	Seki et al. 1991
Discolampa ethion	Rhamnaceae	2	-	0?	Bell 1915, Hinton 1951, Sevastopulo 1973

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Jamides section					
Jamides bochus	Fabaceae Mimosaceae	3	y, i	2**	Matsuoka 1976, Norman 1976 Johnston & Johnston 1980
J. celeno	Caesalpiniaceae Fabaceae Meliaceae	5	y, i	2**	Corbet & Pendlebury 1978, Eliot 1980, pers. obs.
J. pura	Fabaceae Caesalpiniaceae	3	y, i	(2**)	Seki et al. 1991, Nässig, pers. comm.
J. caeruleus	Caesalpiniaceae	3?	y, i	(2**)	Nässig, pers. comm.
J. elpis	Zingiberaceae	3	i	2?(**)	Bell 1915, Sevastopulo 1973
J. alecto	Zingiberaceae	3	i	(2**)	Norman 1976, Seki et al. 1991
J. aleuas	Sapindaceae	2?	?	(2**)	Common & Waterhouse 1981
J. phaseli	Fabaceae	3	y, i, e	2**	Common & Waterhouse 1981
J. cyta	Myrtaceae	2?	i, e	(2?)**	Kirton & Kirton 1987
Catochrysops strabo	Fabaceae + ??	3/4?	i	3(**)	Bell 1915, Corbet & Pendlebury 1978
C. panormus	Fabaceae	2	y, i	3**	Common & Waterhouse 1981
Lampides boeticus	Fabaceae Cistaceae (ov.) Bignoniaceae (ov.)	3/4?	i, f, e	2**	Corbet & Pendlebury 1978, Martín 1984, Thomas & Mallorie 1985, Pelzer 1991
Uranothauma section					
Uranothauma nubifer	Mimosaceae	2	y	0	Jackson 1937
U. delatorum	Mimosaceae	2	y	0	Jackson 1937
U. falkensteini	Mimosaceae	2	y	0?**	Jackson 1937
U. vansomereni	Mimosaceae	2	(y)	?	Sevastopulo 1975
U. confusa	Escalloniaceae (lab)	1?	(y)	?	Kielland 1990
U. crawshayi	Escalloniaceae (lab)	1?	(y)	?	Kielland 1990
U. uganda	Escalloniaceae ?	?	(y)	?	Kielland 1990
U. cuneatum	Myricaceae (lab)	1?	(y)	?	Kielland 1990
U. heritsia	Euphorbiaceae	1?	y	0	Jackson 1937
Phlyaria cyara	Mimosaceae	1?	y	0?**	Jackson 1937
Cacyreus lingeus	Lamiaceae Geraniaceae	4	y, i, f, e	0?*	Clark & Dickson 1971, Sevastopulo 1975
C. virilis	Lamiaceae	3	i	0?*	Clark & Dickson 1971
C. darius	Lamiaceae	2?	(i)	0?	Ackery & Rajan 1990
C. palemon	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. marshalli	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. dicksoni	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. niebuhri	Geraniaceae	2	(i, f, e)	(0)	Larsen 1984
Harpendyreus notobia	Lamiaceae	2	i	0?*	Clark & Dickson 1971
H. tsomo	Lamiaceae	4	(i, f)	?	Pennington et al. 1978
ssp. *noquasa*	Rosaceae		(i, f)	?	Migdoll 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Leptotes section					
Leptotes pirithous	Fabaceae Mimosaceae Caesalpiniaceae Plumbaginaceae Rosaceae, Verbenaceae, Bignoniaceae, Lythraceae ?	5	y, i, f, e	2**	Claassens & Dickson 1980, Martín 1984, Migdoll 1988, Jutzeler, pers. comm.
L. plinius	Mimosaceae Fabaceae Plumbaginaceae	5	i, f	2/3**	Warnecke 1932/33, Sevastopulo 1973
L. pulchra	Mimosaceae Fabaceae	3	(i, f)	(2**)	Stempffer 1967
L. brevidentatus	Fabaceae Plumbaginaceae	4	i, f, e	2**	Clark & Dickson 1971, Ackery & Rajan 1990
L. jeanneli	Fabaceae	3?	(i, f)	(2)**	Clark & Dickson 1956, Ackery & Rajan 1990
L. webbianus	Fabaceae	3	y, i, f	(1)**	Bacallado 1976, Martín 1982, Schurian, pers. comm.
L. mandersi	Fabaceae Caesalpiniaceae	3	(y, i)	(2**?)	Ackery & Rajan 1990
L. cassius	Fabaceae Plumbaginaceae Malpighiaceae	5	i, f	3**	Downey & Allyn 1979
L. marina	Fabaceae Mimosaceae Plumbaginaceae Rosaceae	5	i, f	3**	Ballmer & Pratt 1988
Castalius section					
Castalius rosimon	Rhamnaceae	2	y	2**	Bell 1915, Corbet & Pendlebury 1978
C. (Tuxentius) cretosus	Rhamnaceae	2	y	(2)**	Jackson 1937, van Someren 1974
C. (T.) melaena	Rhamnaceae Fabaceae ?	2/4?	-	(2)**	Clark & Dickson 1971, Ackery & Rajan 1990
C. (T.) calice	Rhamnaceae Fabaceae	4	-	(2)**	Clark & Dickson 1971, Ackery & Rajan 1990
C. (T.) interruptus	Rhamnaceae	2	-	(2**)	Larsen 1984
C. (T.) margaritaceus	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
C. (Caleta) decidia	Rhamnaceae	2	y	2**	Hinton 1951
Tarucus ananda	Rhamnaceae Loranthaceae Oleaceae	4	?	3/4**	Bell 1915, Hinton 1951
T. waterstradti	Rhamnaceae Myrtaceae	4	?	3/4**	Maschwitz et al. 1985b
T. callinara	??	?	?	3(**)	Elfferich, pers. comm.
T. nara	Rhamnaceae	2	?	3/4**	Bell 1915, Sevastopulo 1941, Larsen 1987
T. rosaceus	Rhamnaceae	2	y	3**	Chapman & Buxton 1919

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Tarucus balkanicus	Rhamnaceae	3	?	3*(*)	Wiltshire 1945, 1948
T. theophrastus	Rhamnaceae	2	y	3**	Baz 1988
T. sybaris	Rhamnaceae	2	-	3(**)	Clark & Dickson 1971, Ackery & Rajan 1990
T. grammicus	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
T. thespis	Rhamnaceae Saxifragaceae	4	y	3**	Dickson 1944
T. bowkeri	Rhamnaceae	2	-	(2)**	Clark & Dickson 1971
T. ungemachi	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
T. kiki	Rhamnaceae	2	?	(2**)	Ackery & Rajan 1990
Zintha hintza	Rhamnaceae	2	y	2/3**	Clark & Dickson 1971, van Someren 1974
Zizeeria section					
Zizina otis	Mimosaceae Fabaceae Zygophyllaceae	5	y, i	3**	Corbet & Pendlebury 1978, Seki et al. 1991
Z. labradus	Fabaceae	3	y, i, f	3**	Common & Waterhouse 1981
Z. antanossa	Fabaceae	3	y, i	(3)**	Clark & Dickson 1971
Zizeeria karsandra	Fabaceae Amaranthaceae Molluginaceae Polygonaceae Oxalidaceae Zygophyllaceae	5	y, i, f	2/3**	Common & Waterhouse 1981, Larsen 1990
Z. knysna	Fabaceae Amaranthaceae Chenopodiaceae Oxalidaceae Zygophyllaceae Euphorbiaceae	5	y	3**	Clark & Dickson 1971, Ackery & Rajan 1990
Z. maha	Oxalidaceae	2	(y, i)	3**	Shields 1984, Shirôzu & Hara 1974
Famegana alsulus	Fabaceae	3	y, i	3**	Common & Waterhouse 1981
Actizera lucida	Fabaceae Oxalidaceae	4	i, f	(2)**	Clark & Dickson 1971
A. stellata	Fabaceae Oxalidaceae	4	y, i, f	(2)**	Clark & Dickson 1971, Sevastopulo 1975
Zizula hylax	Fabaceae Oxalidaceae Zygophyllaceae Acanthaceae Verbenaceae	5	y, i, f, e	3**	Bell 1915, Warnecke 1932/33, Clark & Dickson 1971, Ackery & Rajan 1990
Brephidium metophis	Chenopodiaceae	2?	e	(2)**	Clark & Dickson 1971
B. exilis	Chenopodiaceae Aizoaceae Amaranthaceae Solanaceae ?	5	i, f	3**	Fernández Haeger 1988
B. isophthalma	Chenopodiaceae Batidaceae	4	(i, f)	3**	Harvey & Longino 1989
Oraidium barberae	Chenopodiaceae	1?	?	(2**)	Migdoll 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Cupido section					
Everes lacturnus	Fabaceae	3	i, f	2*(*?)	Shirôzu & Hara 1974, Corbet & Pendlebury 1978
E. huegelii	Fabaceae	3	y, i, e	(2*?)	Jones 1938
E. argiades	Fabaceae Cannabaceae ?	3/4	i, f	2**	Iwase 1954
E. amyntula	Fabaceae	3	i, f, e	2**	Ballmer & Pratt 1988
E. comyntas	Fabaceae	3	y, i, f, e	2**	Warnecke 1932/33, Ballmer & Pratt 1988
E. alcetas	Fabaceae	3	i, f	(2)**	SBN 1987
E. decoloratus	Fabaceae	2/3	(i, f)	(2**)	Higgins & Riley 1978
E. pontanini	*Boea*	2?	i	(2)**	Koiwaya 1989
E. (Tongeia) fischeri	Crassulaceae	3	-	3*	Iwase 1954
E. (T.) hainani	Crassulaceae	2	?	(2*)	Uchida 1985
E. (T.) ion	Crassulaceae	2	?	(2)*	Koiwaya 1989
E. (Talicada) nyseus	Crassulaceae	3	e	1(*)	Bell 1915, Larsen 1987, Elfferich, pers. comm.
Cupido minimus	Fabaceae	3	i, f, e	2*	Baylis & Kitching 1988
C. lorquinii	Fabaceae	3	i, f	3*	Munguira & Martín 1989, Devarenne 1990
C. osiris	Fabaceae	2?	i, f	3**	SBN 1987
Pithecops corvus	Fabaceae Rubiaceae	4	(i)	(3**)	Corbet & Pendlebury 1978
P. fulgens	Fabaceae	2?	y, i	3*(*)	Ejima et al. 1978
Azanus jesous	Mimosaceae Fabaceae	3	y, i, f, e	3**	Bell 1915, Migdoll 1988
A. ubaldus	Mimosaceae	2	i, f	3**	Hinton 1951
A. uranus	Mimosaceae	2	i, f	3**	Hinton 1951
A. moriqua	Mimosaceae	2	i, f, e	(3)**	Clark & Dickson 1971
A. occidentalis mirza	Mimosaceae Sapindaceae	4	i, f	(3)**	Clark & Dickson 1971
A. natalensis	Mimosaceae	2	y, i, f, e	3**	Clark & Dickson 1971
A. isis	Mimosaceae	2?	y	(3**)	van Someren 1974
Eicochrysops messapus	Fabaceae Mimosaceae Santalaceae	5	i, f	3**	Sevastopulo 1975, Claassens & Dickson 1980
Ei. hippocrates	Polygonaceae	3	i, f	(3)**	Clark & Dickson 1971
Ei. nandianus	??	?	f	(3**)	Jackson 1937
Lycaenopsis section					
Neopithecops zalmora	Rutaceae	2	y, i, e	2**	Bell 1915, Hinton 1951
N. lucifer	Rutaceae	2	(y, i)	2**	Common & Waterhouse 1981
Megisba strongyle	Sapindaceae Euphorbiaceae Mimosaceae (lab)	5	y, i	(2)**	Lambkin & Samson 1989
M. malaya	Sapindaceae Euphorbiaceae	4	(y, i)	(2**)	Corbet & Pendlebury 1978

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Udara albocaerulea	Rosaceae Symplocaceae Aquifoliaceae Caprifoliaceae	5	i, f	(2)*	Iwase 1954, Shirôzu & Hara 1974
U. dilecta	Fagaceae	1?	?	?	Seki et al. 1991
U. (Vaga) blackburni	Mimosaceae Urticaceae Sapindaceae Rubiaceae	5	i, f	0	Scott 1986
Actyolepis puspa	Fabaceae Caesalpiniaceae Mimosaceae Rosaceae Combretaceae, Sapindaceae, Malpighiaceae, Euphorbiaceae, Ericaceae	5	(i, f)	2*(*)	Shirôzu & Hara 1974, Corbet & Pendlebury 1978, Johnston & Johnston 1980
Celastrina argiolus	Fabaceae Ranunculaceae Polygonaceae Hamamelidaceae Fagaceae, Moraceae, Saxifragaceae, Rosaceae, Lythraceae, Anacardiaceae, Hippocastanaceae, Celastraceae, Rhamnaceae, Araliaceae, Aquifoliaceae, Cornaceae, Ericaceae, Oleaceae, Caprifoliaceae, Lamiaceae, Asteraceae etc.	5	i, f	2**	Scott 1986, Ballmer & Pratt 1988, Jutzeler 1990a
C. ebenina	Rosaceae	1	y, i, f	2(**)	Scott 1986
C. sugitanii	Hippocastanaceae Cornaceae	4	i, f	2*(*)	Iwase 1954, Shirôzu & Hara 1974, Eliot & Kawazoé 1983
C. gigas	Rosaceae	1?	-	0(*)?	Jones 1938
C. huegelii	Rosaceae	1?	-	0(*)?	Jones 1938
C. oreas	Rosaceae	1?	-	0(*)?	Norman 1950, 1976
C. lavendularis	Fabaceae	3	(y)	(2**)	Uchida 1984
Glaucopsyche section					
Glaucopsyche lygdamus	Fabaceae	3	i, f	3**	Ballmer & Pratt 1988
G. piasus	Fabaceae	2	i, f	3**	Ballmer & Pratt 1988
G. lycormas	Fabaceae	2?	i, f	3**	Iwase 1954
G. alexis	Fabaceae	3	i, f	3**	SBN 1987
G. paphos	Fabaceae	1?	(i)	(3**)	Parker 1983
G. melanops	Fabaceae	3	i, f	3**	Martín 1981
Maculinea arion	Lamiaceae	2	i, f	4*	SBN 1987
M. arionides	Lamiaceae	2?	i, f	4(*)	Iwase 1953 & 1954
M. teleius	Rosaceae	2	i, f, e	4*	SBN 1987
M. nausithous	Rosaceae	1	i, f, e	4*	SBN 1987
M. alcon	Gentianaceae	2	i, f, e	4*	SBN 1987
M. rebeli	Gentianaceae	2	i, f, e	4*	SBN 1987
Iolana iolas	Fabaceae	2	i, f, e	2*	SBN 1987, Devarenne 1990
I. alfierii	Fabaceae	1	i, f	(2*)	Larsen 1990
Sinia divina	Fabaceae	1?	i, f	3**	Iwase 1954

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Turanana panagaea	Fabaceae (ov.)	1?	?	(3**)	Schurian & Eckweiler, pers. comm.
T. cytis	Fabaceae ?	1?	?	(3**)	Schurian & Eckweiler, pers. comm.
Pseudophilotes baton	Lamiaceae	3	i, f	2**	SBN 1987
Ps. panoptes	Lamiaceae	3	i, f	(2**)	Nel 1982
Ps. schiffermuelleri	Lamiaceae	2/3	(i, f)	(2)**	Higgins & Riley 1978
Ps. barbagiae	Lamiaceae ?	2?	?	(2**)	de Prins & van der Poorten 1982
Ps. abencerragus	Lamiaceae Fabaceae	4	(i, f)	(2**)	Thomas & Mallorie 1985, Devarenne 1990
Ps. bavius	Lamiaceae	2	i, e	2*(*)	Thomas & Mallorie 1985, König 1988
Ps. sinaicus	Lamiaceae	2	y, i	(2**)	Larsen 1990
Euphilotes enoptes	Polygonaceae	2	y, i, f	3**	Langston & Comstock 1966, Ballmer & Pratt 1988
Eu. mojave	Polygonaceae	2	y, i, f	(3)**	Ballmer & Pratt 1988
Eu. rita	Polygonaceae	2	y, i, f	3**	Ballmer & Pratt 1988
Eu. battoides	Polygonaceae	2	y, i, f	3**	Ballmer & Pratt 1988
Eu. bernardino	Polygonaceae	2	(y, i)	3**	Mattoni 1989
Eu. spaldingi	Polygonaceae	2	y, i, f	(3**)	Scott 1986
Philotiella speciosa	Polygonaceae	1	y, i	(2)*	Ballmer & Pratt 1988
Philotes sonorensis	Crassulaceae	1	e	3**	Shields 1973, Ballmer & Pratt 1988
Scolitantides orion	Crassulaceae	2	e	3**	Chapman 1915c, SBN 1987
Euchrysops section					
Euchrysops cnejus	Fabaceae Mimosaceae	3	i, f, e	3**	Viehmeyer 1910a, Bell 1915, Common & Waterhouse 1981
Eu. osiris	Fabaceae Lamiaceae ?	3/4	y, i, f	3**	Clark & Dickson 1971
Eu. barkeri	Fabaceae Lamiaceae Bignoniaceae ?	5	y, i, e	3**	Clark & Dickson 1971, Ackery & Rajan 1990
Eu. malathana	Fabaceae Myrtaceae Bignoniaceae ?	4/5	y, i	3**	Clark & Dickson 1971, Sevastopulo 1975
Eu. dolorosa	Fabaceae Lamiaceae	4	y, f	1/2**	Clark & Dickson 1971, Henning 1983b
Eu. subpallida	Lamiaceae	2?	(y, i)	(2**)	Ackery & Rajan 1990
Eu. lois	Scrophulariaceae	2?	(y, i)	(2**)	Ackery & Rajan 1990
Eu. subdita crawshayinus	Boraginaceae	3	e	3**	Jackson 1937, Cripps 1947, Kielland 1990
Lepidochrysops lacrimosa	Fabaceae	1?	y	(3)**	Clark & Dickson 1971
L. ariadne	Fabaceae	2?	(i)	(3**)	Pennington et al. 1978
L. patricia	Verbenaceae	2	i	4*	Clark & Dickson 1971
L. (ssp?) *parsimon*	Lamiaceae	2?	(i)	(4*)	Sevastopulo 1975

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Lepidochr. plebeia	Verbenaceae	1?	?	(4*)	Migdoll 1988
L. vansoni	Verbenaceae	2?	(i)	(4*)	Pennington et al. 1978
L. peculiaris	Verbenaceae	2?	i, e	(4*)	Sevastopulo 1975
L. oreas	Selaginaceae	2	i	4*	Claassens & Dickson 1980
L. wykehami	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. titei	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. australis	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. trimeni	Selaginaceae Fabaceae ?	4	y, i	4*	Clark & Dickson 1971
L. asteris	Selaginaceae Lamiaceae	4	i	(4)*	Clark & Dickson 1971
L. barnesi	Lamiaceae ?	?	(i)	(4*)	Pennington et al. 1978
L. ortygia	Selaginaceae Lamiaceae	4?	(i)	(4*)	Migdoll 1988
L. praeterita	Lamiaceae ?	?	(i)	(4*)	Pennington et al. 1978
L. jefferyi	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. tantalus	Lamiaceae	2	(i)	(4*)	Migdoll 1988
L. swanepoeli	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. grahami	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. pephredo	Lamiaceae	2?	(i)	4(*)	Pennington et al. 1978
L. irvingi	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. ignota	Lamiaceae	2	i, f	4*	Henning 1983a
L. letsea	Lamiaceae	1?	(i)	(4*)	Migdoll 1988
L. quassi [as *phasma*]	Lamiaceae	2	i	4*	Farquharson 1922, Chapman 1922
L. forsskali	Lamiaceae	2?	(i)	(4*)	Ackery & Rajan 1990
L. pittawayi	Lamiaceae	2?	(i)	(4*)	Ackery & Rajan 1990
L. variabilis	Selaginaceae Lamiaceae	4	i, e	4*	Cottrell 1965, Clark & Dickson 1971
L. ketsi	Selaginaceae Lamiaceae	4	i, e	(4)*	Cottrell 1965, Clark & Dickson 1971
L. robertsoni	Selaginaceae	2	i, (e)	4(*)	Claassens & Dickson 1980
L. dukei	Selaginaceae	2	i, e (galls)	(4)*	Cottrell 1965
L. bacchus	Selaginaceae	3	y, i, e	(4)*	Cottrell 1965, Clark & Dickson 1971
L. badhami	Geraniaceae (ov.)	?	(i)	(4*)	Pennington et al. 1978
L. puncticilia	Selaginaceae	3	y, i, e	(4*)	Cottrell 1965, Clark & Dickson 1971
L. methymna	Selaginaceae	3	y, i, (e)	4*	Cottrell 1965, Clark & Dickson 1971
L. victoriae	??	?	?	4(*)	Cripps 1947
L. longifalces	??	?	?	4(*)	Cottrell 1984
Oboronia punctatus	Zingiberaceae	2?	i	4(*)	Stempffer 1967
O. guessfeldtii	Zingiberaceae	2?	(i)	(4*)	Pennington et al. 1978
O. bueronica	Zingiberaceae	2?	(i)	(4*)	Kielland 1990
Athysanota ornata	Zingiberaceae ?	2?	?	(3/4*)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Polyommatus section					
Chilades pandava	Fabales Cycadaceae	5	(y)	3**	Hinton 1951, Corbet & Pendlebury 1978
Ch. mindora [as *kiamurae*]	Cycadaceae	1?	y, e	(2**)	Wakabayashi & Yoshizaki 1967
Ch. lajus	Rutaceae + Aphididae!	3	y	2/3**	Bell 1915, Agarwala & Saha 1984
Ch. trochylus	Fabaceae Euphorbiaceae Boraginaceae	5	y, i, f, e	3**	Clark & Dickson 1971, Larsen 1990, Wasserthal, pers. comm.
Ch. parrhasius	Caesalpiniaceae Mimosaceae	3	i, f	3**	Larsen 1980, 1984
Ch. galba	Caesalpiniaceae	3	(i)	3(**)	Larsen & Nakamura 1983
Ch. kedonga	Mimosaceae (ov.)	2?	y, i	(3**)	van Someren 1974
Ch. eleusis	Mimosaceae	2?	(y, i)	(3**)	Ackery & Rajan 1990
Plebejus saepiolus	Fabaceae	2	i, f	(3)**	Ballmer & Pratt 1988
P. argus	Fabaceae Cistaceae Ericaceae Geraniaceae (lab) Lamiaceae ? Asteraceae ?	5	i	3/4**	Thomas 1985, pers. observ.
P. (Plebejides) martini	Fabaceae Ericaceae ?	2/4?	(y)	3**	Thomas & Mallorie 1985, Rojo de la Paz pers. comm.
P. (P.) hespericus	Fabaceae	2	(y)	3**	Munguira & Martín 1989, Bálint 1991
P. (P.) trappi	Fabaceae	2	y	3**	SBN 1987, Bálint 1991
P. (P.) sephirus	Fabaceae	2	y	3**	Bálint & Kertész 1990, pers. observ.
P. (P.) pylaon	Fabaceae	2	(y)	3(**)	Bálint & Kertész 1990, Bálint 1991
P. (P.) philbyi	Fabaceae	2	(y)	3(**)	Bálint & Kertész 1990, Bálint 1991
P. vogelii	Geraniaceae	1?	i	(3**)	Thomas & Mallorie 1985, Devarenne 1990
P. (Lycaeides) idas	Fabaceae Elaeagnaceae Cistaceae Empetraceae Ericaceae	5	y, i	3/4**	SBN 1987, Ballmer & Pratt 1988, Jutzeler 1989d, 1990b
P. (L.) melissa	Fabaceae	3	y, i	3**	Ballmer & Pratt 1988
P. (L.) argyrognomon	Fabaceae	3	i, f	3**	SBN 1987
P. (L.) subsolana	Fabaceae	3	y	3**	Iwase 1954, Hama et al. 1989
Plebejus (Icaricia) icarioides	Fabaceae	2	y, i, f	3**	Ballmer & Pratt 1988
P. (I.) acmon	Fabaceae Polygonaceae	4	y, i, f	3**	Ballmer & Pratt 1988
P. (I.) lupini	Polygonaceae	2	i	3**	Ballmer & Pratt 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
P. (Icaricia) shasta	Fabaceae	3	y, i	3**	Emmel & Shields 1980
P. (I.) neurona	Polygonaceae	2	(y, i)	(3)**	Ballmer & Pratt 1988
P. (Plebulina)					
emigdionis	Chenopodiaceae Fabaceae ?	1/3?	-	3**	Scott 1986, Ballmer & Pratt 1988
P. (Vacciniina)					
optilete	Ericaceae	2	y, i	0	SBN 1987
P. (V.) loewii	Fabaceae	2	y, i	?	Larsen 1990, Schurian, pers. comm.
P. (V.) morgiana [as *hyrcana*]	Fabaceae (ov.)	2?	y	?	Eckweiler 1981
P. (V.) kwaja	Fabaceae	1?	?	?	Eckweiler, pers. comm.
P. (Kretania)					
psylorita	Fabaceae	1?	?	?	Hemmersbach 1989, Leigheb et al. 1990
Polyommatus (Albulina)					
orbitulus	Fabaceae	3	?	(2)**	SBN 1987
P. (Agriades)					
franklinii	Primulaceae	1?	e	0	Ballmer & Pratt 1988
P. (A.) glandon	Primulaceae	2/3	i	0	SBN 1987
P. (A.) zuellichi	Primulaceae	1	y, i	0	Munguira & Martín 1989a
P. (A.) aquilo	Saxifragaceae Diapensiaceae (ov.) Ericaceae (ov.) Fabaceae ?	5	i	0	Higgins & Riley 1978, Scott 1986, Klassen et al. 1989
P. (A.) pyrenaicus	Primulaceae	3	y, i	0	Chapman 1915a, Martín 1982
P. (A.) ergane	Primulaceae	1	y, i	0	Pljushtch 1989
P. (Aricia)					
agestis	Geraniaceae Cistaceae	4	y, i	3**	SBN 1987
P. (A.) artaxerxes	Geraniaceae Cistaceae	4	y, i	3**	SBN 1987
P. (A.) cramera	Geraniaceae Cistaceae	4	(i, f)	3**	Martín 1982, Thomas & Mallorie 1985
P. (A.) morronensis	Geraniaceae	2	y, i	3**	Munguira & Martín 1988
P. (A.) nicias	Geraniaceae	2	i, f	(3)**	SBN 1987
P. (A.) anteros	Geraniaceae	2	(i, f)	(3**)	Schurian, pers. comm.
P. (A.) isaurica	Geraniaceae	2	i, f	(3)**	Schurian, pers. comm.
P. (A.) hyacinthus	Geraniaceae	2	i	(3)**	Schurian & Rose 1991
P. (A.) vandarbani	Geraniaceae (ov.)	2?	(i)	(3**)	Schurian & Rose 1991
P. (A.) eumedon	Geraniaceae	2	i, f	3**	SBN 1987
P. (Agrodiaetus)					
damon	Fabaceae	2	i, f	3**	SBN 1987
P. (A.) humedasae	Fabaceae	2	(i)	(3)**	Manino et al. 1987
P. (A.) ainsae	Fabaceae	2?	?	(3**)	Martín 1982
P. (A.) dolus	Fabaceae	2	i, f	3**	Martín 1982
P. (A.) antidolus	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Polyommatus (Agrodiaetus) ripartii	Fabaceae	2	i, f	3**	Martín 1982
P. (A.) admetus	Fabaceae	2	(i, f)	(3)**	Higgins & Riley 1978
P. (A.) fabressei	Fabaceae	2?	?	(3**)	Martín 1982
P. (A.) carmon	Fabaceae (ov.)	2?	?	(3**)	Schurian, pers. comm.
P. (A.) turcicus	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) mithridates	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) baytopi	Fabaceae	2	?	(3**)	Schurian & Eckweiler, pers. comm.
P. (A.) hopfferi	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) firdussii	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) dama	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) hamadanensis	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) transcaspica	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) phyllis	Fabaceae (ov.)	1?	?	(3**)	Schurian, pers. comm.
P. (A.) actis	Fabaceae ?	1?	?	(3**)	Eckweiler & Görgner 1981
P. (A.) bogra ?	Fabaceae	1?	?	3(**)	Eckweiler, pers. comm.
P. (A.) glaucias	Fabaceae (ov.)	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) thersites	Fabaceae	2	(y)	3**	Martín 1982
P. (A.) semiargus	Fabaceae	3	y, i	3**	SBN 1987
P. (A.) helena	Fabaceae	1?	y, i	(3**)	Brown 1977
P. (A.) corona	Fabaceae (ov.)	2?	?	(3**)	Schurian, pers. comm.
P. (A.) coelestina	Fabaceae (ov.)	2?	?	(3**)	Eckweiler & Görgner 1981, Schurian et al. 1991
P. (A.) diana	Fabaceae (ov.)	2	?	(3**)	Schurian et al. 1991, Eckweiler, pers. comm.
P. (A.) ellisoni	Fabaceae	2?	(y, i)	(2**)	Paulus & Rose 1971, Larsen 1974
P. (A.) myrrha	Fabaceae	2?	?	(3**)	Eckweiler & Görgner 1981, Schurian et al. 1991
P. (Lysandra) coridon	Fabaceae	2	–	3**	SBN 1987
P. (L.) hispana	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) albicans	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) ossmar	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) corydonius	Fabaceae	2	–	(3)**	Schurian 1989a
P. (L.) bellargus	Fabaceae	2	–	3**	Thomas 1983
P. (L.) punctifera	Fabaceae	2	y	3**	Schurian & Thomas 1985
P. (L.) amandus	Fabaceae	2	(y, i)	3**	SBN 1987
P. (L.) escheri	Fabaceae	2	y, i	3**	Chapman 1915b, SBN 1987
P. (L.) dorylas	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) golgus	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) nivescens	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) atlantica	Fabaceae	1?	(i, f)	(3**)	Thomas & Mallorie 1985
P. (Meleageria) daphnis	Fabaceae	2	–	3**	SBN 1987
P. (Polyommatus) icarus	Fabaceae Geraniaceae ?	3/4?	i	2/3**	Martín 1984, SBN 1987, Bálint, pers. comm.
P. eros	Fabaceae	3	y, i	2/3**	SBN 1987, Jutzeler 1989a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hemiargus ceraunus	Fabaceae Caesalpiniaceae Polygonaceae Marantaceae	5	y, i, f	3**	Ehrlich & Raven 1964, Ballmer & Pratt 1988
H. isola	Fabaceae Mimosaceae	3	y, i, f	3**	Scott 1986
H. thomasi	Caesalpiniaceae Sapindaceae Rubiaceae ?	4/5	i, f, e	(3**)	Scott 1986
H. ammon	Caesalpiniaceae	2?	(y, i)	(3**)	Riley 1975
H. hanno	Oxalidaceae	2?	(y, i)	(3**)	Barcant 1970

Note: The author has put special efforts into the accuracy and completeness of the above compilation. However, in view of the tremendous bulk of literature records that had to be evaluated, this listing will certainly not be free of errors, and the author takes full responsibility for all faults and inaccuracies that may have accumulated in the course of compilation. In particular, this holds for all hypothetical assignments. Any corrections and additions will be greatly acknowledged.

Table 18: Systematic synopsis of the hostplant taxa of the Lycaenidae and numbers of species certainly recorded to utilize them. See Table 17 for detailed records.

Taxon	Number
PTERIDOPHYTA	
Polypodiaceae	2
CONIFEROPHYTINA	
Pinaceae	5
Cupressaceae	7
CYCADOPHYTINA	
Cycadaceae	8
MAGNOLIOPHYTINA	
MAGNOLIIDAE	
Annonaceae	3
Lauraceae	13
Cassythaceae	1
Piperaceae	1
RANUNCULIDAE	
Ranunculaceae	2
CARYOPHYLLIDAE	
Molluginaceae	1
Phytolaccaceae	1
Batidaceae	1
Aizoaceae	3
Cactaceae	1
Portulacaceae	1
Chenopodiaceae	9
Amaranthaceae	4
Polygonaceae	58
Plumbaginaceae	5
HAMAMELIDIDAE	
Hamamelidaceae	2
Fagaceae	48
Betulaceae	4
Corylaceae	3
Myricaceae	5
Juglandaceae	6
Casuarinaceae	1
Ulmaceae	10
Moraceae	12
Cannabaceae	1
Urticaceae	2
ROSIDAE	
Cunoniaceae	1
Grossulariaceae	1
Saxifragaceae	4
Crassulaceae	19
Escalloniaceae	3
Bruniaceae	1
Rosaceae	50
Chrysobalanaceae	4
Fabales	321
Proteaceae	15
Lythraceae	8
Myrtaceae	29
Barringtoniaceae	1
Punicaceae	5
Lecythidaceae	7
Melastomataceae	10
Rhizophoraceae	3
Combretaceae	27
Rutaceae	8
Simaroubaceae	4
Anacardiaceae	19
Meliaceae	3
Sapindaceae	55
Hippocastanaceae	4
Aceraceae	1
Melianthaceae	2
Coriariaceae	1
Oxalidaceae	9
Erythroxylaceae	1
Malpighiaceae	12
Zygophyllaceae	21
Geraniaceae	18
Connaraceae	3
Celastraceae	3
Hippocrateaceae	1
Rhamnaceae	43
Santalaceae	3
Olacaceae	12
Loranthaceae	100
Euphorbiaceae	37
Thymelaeaceae	3
Elaeagnaceae	3
Pittosporaceae	3
Araliaceae	2
Apiaceae	1

DILLENIIDAE	
Theaceae	2
Hypericaceae	2
Ochnaceae	1
Dipterocarpaceae	1
Flacourtiaceae	1
Cistaceae	8
Salicaceae	6
Begoniaceae	2
Cucurbitaceae	3
Tiliaceae	4
Elaeocarpaceae	1
Sterculiaceae	18
Malvaceae	10
Ebenaceae	3
Styracaceae	1
Symplocaceae	3
Sapotaceae	9
Myrsinaceae	6
Primulaceae	5
Aquifoliaceae	3
Cornaceae	3
Ericaceae	19
Empetraceae	1
Epacridaceae	3
Diapensiaceae	1

LAMIIDAE	
Caprifoliaceae	7
Oleaceae	12
Gentianaceae	2
Apocynaceae	1
Asclepiadaceae	1
Loganiaceae	3
Rubiaceae	18
Solanaceae	15
Convolvulaceae	4
Hydrophyllaceae	1
Boraginaceae	13
Loasaceae	1
Scrophulariaceae	3
Bignoniaceae	11
Acanthaceae	2
Gesneriaceae	1
Myoporaceae	1
Plantaginaceae	1
Verbenaceae	29
Lamiaceae	37
Selaginaceae	14

ASTERIDAE	
Asteraceae	27

LILIIDAE	
Dioscoreaceae	10
Smilacaceae	4
Agavaceae	2
Haemodoraceae	1
Alliaceae	2
Amaryllidaceae	1
Liliaceae	2
Alstroemeriaceae	1
Orchidaceae	5
Bromeliaceae	8
Musaceae	2
Strelitziaceae	1
Zingiberaceae	5
Marantaceae	1
Flagellariaceae	2
Poaceae	1

ARECIDAE	
Arecaceae	3

Table 19: List of recorded ant-associations of the Lycaenidae (basically field observations, exceptional laboratory records = **lab**). Only records where the ants have been determined to genus level at least are incorporated. Systematic arrangement and nomenclature (first column), as well as presence of larval ant-organs and estimated degrees of myrmecophily (second column), are the same as in Table 17.

Third column: Associated ant genera or species according to the determinations given in the references cited. If reference is only made to a species-group within an ant genus, this is indicated by "**gr.**" following the species name. " ?" inserted before the species name: uncertain species determinations. " ?" following a species name: questionable determinations or doubtful records. Associations refer to caterpillars if not stated otherwise (**ad.** = adults, **ov.** = oviposition). Included are the few records where ants have been observed to behave indifferently towards the larvae (**indiff.**, e.g. Miletinae in ant-tended homopteran aggregations), or where attacks have been reported. Only those references are cited (fourth column) where appropriate information on the identity of associated ants is given (for further information see Table 17).

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Poritiinae:			
Liptenini:			
Liptena undina	0/4?	*Crematogaster* sp.	Jackson 1937
Teratoneura isabellae	0/4?	*Crematogaster* sp.	Farquharson 1922
Deloneura ochrascens	0/4??	*Crematogaster* sp.	Jackson 1937
Iridana perdita marina	0/4?	*Crematogaster* sp.	Jackson 1937
Epitola (Aethiopana) honorius	3?	*Crematogaster* sp.	Farquharson 1922
E. (Epitola) urania	0/3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. carcina	3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. ceraunia	3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. elissa	3?	*Crematogaster* sp.	Ackery & Rajan 1990
Miletinae:			
Miletini:			
Spalgis lemolea	0	*Crematogaster* sp. *Oecophylla longinoda* *Anaplocnemis* sp. (all indiff., at homopterans)	Cottrell 1984
Miletus chinensis	0/3?	*Dolichoderus bituberculatus* *Polyrhachis dives* (?)	Kershaw 1905
M. boisduvali	0/3?	*Dolichoderus* sp. *Polyrhachis* sp. (?)	Roepke 1919, Cottrell 1984
M. biggsii	0/4?	*Dolichoderus* sp.	Maschwitz et al. 1985a, 1988
M. symethus	0/4?	*Dolichoderus* sp.	Eliot 1980
Allotinus unicolor	0/3?	*Anoplolepis longipes* (indiff., ov.)	Maschwitz et al. 1985a, Fiedler & Maschwitz 1989c
A. subviolaceus	0	*Anoplolepis longipes* (indiff.)	Maschwitz et al. 1988
A. major	0	*Anoplolepis longipes* (indiff., ov.)	Kitching 1987

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Allotinus davidis	0	*Crematogaster difformis* (indiff.)	Maschwitz et al. 1985a
A. substrigosus	0	*Crematogaster* sp. (ad.) *Technomyrmex* sp. (indiff.)	Maschwitz et al. 1985a, 1988
A. apries	4?	*Myrmicaria lutea*	Maschwitz et al. 1988
Logania malayica	0?	*Leptothorax* sp. (indiff., ad.)	Maschwitz et al. 1988
Megalopalpus zymna	0	*Pheidole aurivillii* (indiff.)	Ackery 1990
Lachnocnema bibulus	0/4?	*Crematogaster* sp. *Pheidole* sp. (both indiff.)	Cottrell 1984
		Camponotus acvapimensis *C. maculatus*	Farquharson 1922, Cripps & Jackson 1940
L. brimo	0	*Camponotus* sp. (indiff.)	Ackery & Rajan 1990
Thestor dicksoni	4	*Anoplolepis custodiens*	Clark & Dickson 1971
Th. basutus	4	*Anoplolepis custodiens*	Clark & Dickson 1971
Th. obscurus	4?	*Anoplolepis custodiens*	Claassens & Dickson 1980
Euliphyra mirifica	4	*Oecophylla longinoda*	Cottrell 1984
Eu. leucyania	4	*Oecophylla longinoda*	Dejean 1991
Liphyra brassolis	4	*Oecophylla smaragdina*	Cottrell 1987
Aslauga lamborni	0[T]	*Crematogaster* sp. (indiff.)	Ackery & Rajan 1990
A. vininga	0[(T)]	*Crematogaster* sp. (indiff.)	Ackery & Rajan 1990
Curetinae:			
Curetis regula	0/2?[T]	*Anoplolepis longipes*	DeVries 1984
Lycaeninae:			
Aphnaeini:			
Spindasis ella	3/4**	*Crematogaster castanea*	Clark & Dickson 1971
S. natalensis	4**	*Crematogaster castanea*	Clark & Dickson 1971
S. nyassae	4**	*Crematogaster* sp.	Hinton 1951
S. avriko	4(**)	*Pheidole* sp.	van Someren 1974
S. tavetensis	4(**)	*Pheidole* sp.	van Someren 1974
S. namaqua	4**	*Crematogaster* sp.	Henning 1983a
S. phanes	4**	*Crematogaster castanea*	Henning 1983a
S. lohita	3/4**	*Crematogaster* sp.	Hinton 1951
S. vulcanus	3/4**	*Crematogaster* sp. / *Pheidole quadrispinosa*	Hinton 1951
S. takanonis	4**	*Crematogaster laboriosa*	Cottrell 1984
Cigaritis zohra	4**	*Crematogaster laestrygon*	Rojo de la Paz 1990
C. allardi	3**	*Crematogaster auberti* *C. antaris* *C. scutellaris*	Rojo de la Paz 1990
C. (Apharitis) acamas	4**	*Crematogaster* sp.	Larsen & Pittaway 1982
C. (A.) myrmecophila	4**	*Crematogaster auberti* *Cataglyphis bicolor* ??	Hinton 1951
Axiocerses amanga	3**	*Camponotus niveosetosus*	Jackson 1937
A. harpax	4**	*Crematogaster* sp. *Pheidole* sp.	Jackson 1947, van Someren 1974

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Axiocerses (Chloroselas) pseudozeritis	4**	*Crematogaster gerstaeckeri*	Jackson 1937
Phasis thero	4*	*Crematogaster peringueyi*	Clark & Dickson 1971
Ph. braueri	4*	*Crematogaster* sp.	Clark & Dickson 1971
Ph. clavum	4*	*Crematogaster* sp.	Clark & Dickson 1971
Aloeides thyra	4(*)T	*Acantholepis capensis*	Claassens & Dickson 1980
A. dentatis	4T	*Acantholepis capensis*	Henning 1983b
A. rossouwi	4(**)	*Acantholepis* sp.	Henning & Henning 1982
Erikssonia acraeina	4**	*Acantholepis* sp.	Henning 1984
Poecilmitis lycegenes	4**	*Crematogaster liengmei*	Henning 1983a
P. aureus	4**	*Crematogaster* sp.	Henning 1983a
P. chrysaor	4**	*Crematogaster liengmei*	Dickson 1943
P. felthami	4**	*Crematogaster* sp.	Clark & Dickson 1971
P. pyroeis	4**	*Camponotus (Tanaemyrmes) dicksoni*	Clark & Dickson 1971
P. palmus	3/4**	*Crematogaster peringueyi*	Claassens & Dickson 1980
P. thysbe	4**	*Crematogaster peringueyi*	Clark & Dickson 1971
P. brooksi	4**	*Crematogaster peringueyi*	Henning 1983a
P. perseus	4(**)	*Crematogaster* sp.	Ackery & Rajan 1990
P. nigricans	4**	*Crematogaster* sp.	Claassens & Dickson 1980
P. lysander	(4)**	*Crematogaster* sp.? (pupa)	Clark & Dickson 1971
P. kaplani	(4**)	*Crematogaster* sp.	Henning 1979
Oxychaeta dicksoni	4(*?)T	*Crematogaster peringueyi*	Clark & Dickson 1971
Lycaenini:			
Lycaena heteronea	2	*Formica pilicornis*	Ballmer & Pratt 1988
L. rubidus	2	*Formica altipetens*	Funk 1975
L. xanthoides	2	*Formica pilicornis*	Ballmer & Pratt 1988
L. editha	2	*Formica altipetens*	Ballmer & Pratt 1988
L. dispar	1	*Myrmica rubra*	Hinton 1951
Theclini:			
Lucia limbaria	3/4(**)	*Iridomyrmex (gracilis* gr.)	Common & Waterhouse 1981
Paralucia aurifera	4**	*Iridomyrmex ?nitidiceps*	Common & Waterhouse 1981
P. spinifera	4**	*Iridomyrmex* sp.	Braby 1990
P. pyrodiscus	4**	*Notoncus enormis* *N. ectatommoides*	Braby 1990
Pseudodipsas eone	3(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
Ps. cephenes	3(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
Acrodipsas cuprea	4(*)	*Iridomyrmex* sp. *Crematogaster* sp.	Common & Waterhouse 1981 Cottrell 1984
A. myrmecophila	4*	*Iridomyrmex (nitidus* gr.)	
A. illidgei	4*	*Crematogaster (laeviceps* gr.)	Samson 1989
Hypochrysops apollo	4(**)	*Iridomyrmex cordatus* *Pheidole megacephala* (indiff.)	Common & Waterhouse 1981
H. arronica	4(**)	*Iridomyrmex scrutator*	Sands 1986
H. plotinus	4(**)	*Iridomyrmec cordatus*	Sands 1986
H. architas	3(**)	*Iridomyrmex cordatus*	Sands 1986
H. halyaetus	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. cyane	3/4(**)	*Iridomyrmex itinerans*	Common & Waterhouse 1981

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Hypochrysops epicurus	3/4(**)	*Iridomyrmex ?nitidiceps*	Common & Waterhouse 1981
H. delicia	3/4(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. ignitus	4**	*Iridomyrmex* (*nitidus* gr.)	Common & Waterhouse 1981
H. piceatus	3(**)	*Iridomyrmex* (*itinerans* gr.)	Common & Waterhouse 1981
H. miskini	4(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
H. digglesii	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. apelles	4**	*Crematogaster* sp.	Common & Waterhouse 1981
H. dicomas	4(**)	*Iridomyrmex* sp. (ov.)	Sands 1986
H. polycletus	4?(**)	*Iridomyrmex* sp. (ov.)	Sands 1986
H. theon	3/4(**)	*Iridomyrmex cordatus*	Common & Waterhouse 1981
Ogyris genoveva	4**	*Camponotus nigriceps*	Common & Waterhouse 1981,
		C. (*consobrinus* gr.)	Pierce & Elgar 1985
		C. perthianus	
		Iridomyrmex purpureus (attacked: Samson & O'Brien 1980)	
O. zosine	3**	*Camponotus claripes*	Hinton 1951,
		Oecophylla smaragdina	Common & Waterhouse 1981
O. idmo	3/4(**)	*Camponotus nigriceps*	Common & Waterhouse 1981
O. otanes	4**	*Camponotus* (*Myrmophyma*) *ferruginipes*	Common & Waterhouse 1981
O. abrota	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
		Froggatella kirbyi	
		Technomyrmex ?albipes	
O. olane	2(**)	*Crematogaster* sp.	Common & Waterhouse 1981
O. ianthis	3(**)	*Froggatella kirbyi*	Common & Waterhouse 1981
O. iphis	3(**)	*Froggatella kirbyi*	Common & Waterhouse 1981
O. aenone	3(**)	*Pheidole* sp.	Common & Waterhouse 1981
		Iridomyrmex (*itinerans* gr.)	
O. amaryllis	3/4**	*Iridomyrmex* (*nitidiceps* gr.)	Common & Waterhouse 1981,
		I. (*rufoniger* gr.)	Aston & Dunn 1985
		Camponotus sp.	
		Crematogaster sp.	
Zesius chrysomallus	4*(*)	*Oecophylla smaragdina*	Hinton 1951
Jalmenus evagoras	4**	*Iridomyrmex anceps*	Pierce 1989
		I. (*rufoniger* gr.)	
J. eichhorni	3**	*Iridomyrmex* sp.	Common & Waterhouse 1981
J. ictinus	4**	*Iridomyrmex purpureus*	Pierce 1989
J. pseudictinus	4**	*Froggatella kirbyi*	Pierce 1989
J. daemeli	4**	*Iridomyrmex* (*rufoniger* gr.)	Pierce 1989
J. inous	3**	*Iridomyrmex ?gracilis*	Common & Waterhouse 1981
J. icilius	3/4**	*Iridomyrmex* (*rufoniger* gr.)	Common & Waterhouse 1981
J. clementi	2/3**	*Iridomyrmex* sp.	Common & Waterhouse 1981
Pseudalmenus chlorinda	3/4**	*Iridomyrmex foetans*	Common & Waterhouse 1981
Arhopala amphimuta	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. moolaiana	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. zylda	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. amantes	4?(**)	*Oecophylla smaragdina*	Bell 1915
A. pseudocentaurus	4**	*Oecophylla smaragdina*	Kirton & Kirton 1987
A. centaurus	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Arhopala micale	3**	*Oecophylla smaragdina*	Common & Waterhouse 1981
Thaduka multicaudata	2/3**	*Crematogaster* sp.	Hinton 1951
Flos fulgida	3**	*Hypoclinea* sp.	Ballmer & Pratt in press
Surendra vivarna	3**	*Anoplolepis longipes*	Maschwitz et al. 1985b
Thecla betulae	1/3	*Lasius niger* (pupae)	Emmet & Heath 1990
Shirozua jonasi	4	*Lasius spathepus*	Pierce & Elgar 1985
Quercusia quercus	0/2	*Lasius* sp.? (pupae)	Emmet & Heath 1990
Eumaeini:			
Catapaecilma elegans	3**	*Crematogaster* sp.	Hinton 1951
Myrina silenus	3**	*Camponotus* sp.	Henning 1983a
M. subornata	(2)**	*Pheidole rotundata* (lab)	Hinton 1951
Loxura atymnus	3**	*Oecophylla smaragdina* *Anoplolepis longipes* (ov.)	Hinton 1951, Maschwitz & Fiedler, pers. obs.
Eooxylides tharis	3**	*Anoplolepis longipes*	Maschwitz & Fiedler, pers. obs.
Drupadia theda	3**	*Crematogaster difformis*	Maschwitz et al. 1985b
D. ravindra	3**	*Tetramorium* sp.	Maschwitz & Fiedler, pers. obs.
Iolaus (Iolaphilus) alcibiades	0/2?	*Crematogaster buchneri* ?	Hinton 1951
I. (I.) julus	2*	*Crematogaster buchneri*	Hinton 1951
I. (Epamera) maesa	3(**)	*Crematogaster buchneri*	Farquharson 1922
Remelana jangala	3*	*Polyrhachis dives*	Young 1991
Hypolycaena erylus	4*	*Oecophylla smaragdina*	Jacobson 1912
H. phorbas	4*	*Oecophylla smaragdina*	Common & Waterhouse 1981
H. philippus	3*	*Camponotus acvapimensis* *C. maculatus* *Pheidole rotundata*	Hinton 1951
H. nigra	3(*)	*Pheidole aurivillii*	Hinton 1951
H. lebona	3*(*)	*Pheidole aurivillii*	Hinton 1951
Deudorix dinochares	2/3*(*)	*Pheidole* sp.	Ackery & Rajan 1990
D. ecaudata	3(*)	*Pheidole* sp.	Sevastopulo 1975
D. suk	3(*)	*Pheidole* sp.	Sevastopulo 1975
D. obscura	3(*)	*Crematogaster buchneri*	Hinton 1951
Rapala pheretima	3(**)	*Oecophylla smaragdina*	Norman 1976
R. iarbus	3**	*Anoplolepis longipes*	Fiedler, pers. obs.
R. manea	3**	*Crematogaster* sp.	Hinton 1951
Tomares ballus	2**	*Plagiolepis pygmaea*	Chapman & Buxton 1919
Arawacus lincoides [as *aetolus*]	3*	*Ectatomma tuberculatum* *E. ruidum*	Robbins & Aiello 1982, Robbins, in press
Rekoa palegon	3*	*Azteca* sp.	DeVries, pers. comm.

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Harkenclenus titus	2*	*Formica subsericea*	Harvey & Webb 1980
		Camponotus nearcticus	
Satyrium edwardsii	3*	*Formica integra*	Webster & Nielsen 1983
S. ilicis	2*	*Camponotus aethiops*	Malicky 1969b, SBN 1987
S. esculi	3*	*Camponotus cruentatus*	Martín & Gurrea 1983
S. fuliginosum	3*	*Formica* (*rufa* gr.)	Ballmer & Pratt 1988
Panthiades bitias	3(*)	*Camponotus* sp.	Callaghan 1982
Tmolus echion	3*	*Ectatomma* sp. (ov.)	Robbins & Aiello 1982
Polyommatini:			
Candalides margarita	2**	*Technomyrmex sophiae*	Common & Waterhouse 1981
C. heathi	2**	*Iridomyrmex* (*gracilis* gr.)	Common & Waterhouse 1981
C. (*Adaluma*) *urumelia*	3**	*Monomorium* sp.	Edwards 1980
		(no larvae on plants with *Oecophylla smaragdina*)	
Anthene emolus	4**	*Oecophylla smaragdina*	Fiedler & Maschwitz 1989
A. seltuttus	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981
A. lycaenina	2/3**	*Oecophylla smaragdina*	Hinton 1951
		Camponotus sp.	
A. lycaenoides	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981
A. definita	2**	*Iridomyrmex* sp.	Claassens & Dickson 1980
A. pitmani	3**	*Crematogaster gerstaeckeri*	Jackson 1937
A. lunulata	3**	*Pheidole* sp.	Farquharson 1922,
		Technomyrmex detorquens	Jackson 1937
		Camponotus acvapimensis	
A. amarah	3**	*Crematogaster bequaerti*	Jackson 1937,
		Pheidole sp.	Milton 1990
		Myrmicaria sp.	
		Acantholepis affinis	
A. larydas	3**	*Crematogaster striatula*	Hinton 1951
		Pheidole aurivillii	
		Camponotus acvapimensis	
A. otacilia	3**	*Crematogaster* sp.	van Someren 1974
A. hodsoni	3(**)	*Pheidole* sp.	van Someren 1974
A. levis	4**	*Crematogaster* sp.	Ackery & Rajan 1990
A. sylvanus	3**	*Pheidole* sp.	Ackery & Rajan 1990
		Camponotus sp.	
A. lachares	3**	*Pheidole aurivillii*	Hinton 1951
		Ph. rotundata	
A. flavomaculatus	3*(*)	*Odontomachus haematodes*	Hinton 1951
		Crematogaster buchneri	
		Pheidole rotundata (lab)	
A. ? alberta	3(**)	*Crematogaster* sp.	Ackery & Rajan 1990
Triclema lucretilis	3(*)	*Crematogaster buchneri*	Hinton 1951
T. nigeriae	4**	*Crematogaster bequaerti*	Jackson 1937
		Pheidole rotundata (lab)	
Neurypexina lyzianus	3(**)	*Pheidole* sp.	Ackery & Rajan 1990
Niphanda fusca	4**	*Camponotus japonicus*	Iwase 1953

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Nacaduba berenice	3**	*Solenopsis ?geminata* (lab)	Bean 1988
N. pactolus	2**	*Camponotus compressus*	Bean 1964, 1988
		Prenolepis sp.: indiff. (lab)	
		Crematogaster sp.: weakly attracted (lab)	
Prosotas dubiosa	2/3**	*Anoplolepis longipes*	Cassidy 1990
Theclinesthes onycha	2/3**	*Iridomyrmex glaber*	Common & Waterhouse 1981
		Notoncus ectatommoides	
		Paratrechina ?bourbonica	
		Polyrhachis (*ammon* gr.)	
Th. miskini	3**	*Oecophylla smaragdina*	Sibatani & Grund 1978,
		Crematogaster sp.	Common & Waterhouse 1981
Th. albocincta	3**	*Rhytidoponera metallica*	Grund & Sibatani 1975
		Iridomyrmex sp.	
		Camponotus sp.	
		Notoncus ?gilberti	
		Polyrhachis (Campomyrma) sp.	
Jamides bochus	2**	*Technomyrmex albipes*	Matsuoka 1976
J. celeno	2**	*Camponotus variegatus*	Corbet & Pendlebury 1978
Lampides boeticus	2**	*Camponotus compressus*	Hinton 1951,
		C. cruentatus	Claassens & Dickson 1980,
		C. sylvaticus	Martín Cano 1984, Schroth &
		C. foreli	Wiemers, pers. comm.
		Prenolepis clandestina	
		Lasius sp.	
		Acantholepis capensis	
		Plagiolepis sp.	
		Tapinoma melanocephalum	
		Iridomyrmex sp. (*humilis?)*	
		Dolichoderus bituberculatus (indiff.)	
Leptotes plinius	2/3**	*Crematogaster* sp.	Bell 1915
L. marina	3**	*Iridomyrmex humilis*	Ballmer & Pratt 1988
L. cassius	3**	*Crematogaster ashmeadi*	Downey & Allyn 1979
		Pheidole anastasii	
		Brachymyrmex heeri	
		Paratrechina bourbonica	
Castalius rosimon	2**	*Prenolepis* sp.	Hinton 1951
Tarucus ananda	3/4**	*Crematogaster* sp.	Bell 1915, Hinton 1951
T. waterstradti	3/4**	*Crematogaster* sp.	Maschwitz et al. 1985b
T. callinara	3(**)	*Crematogaster* sp.	Elfferich, pers. comm.
T. nara	3/4**	*Crematogaster* sp.	Bell 1915, Sevastopulo 1941,
		Pheidole latinoda	Hinton 1951
		Camponotus compressus	
T. rosaceus	3**	*Monomorium salomonis*	Chapman & Buxton 1919,
		Plagiolepis pygmaea	Rojo de la Paz,
		Camponotus sicheli	pers. comm.
T. thespis	3**	*Iridomyrmex humilis*	Claassens & Dickson 1980
Zintha hintza	2/3**	*Crematogaster jeanneli*	Jackson 1937
		Technomyrmex detorquens	

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Zizeeria karsandra	2/3**	*Tapinoma melanocephalum*	Corbet & Pendlebury 1978
Z. knysna	3**	*Tapinoma melanocephalum*	Warnecke 1932/33,
		Lasius niger (lab)	Elfferich, pers. comm.
Z. maha	3**	*Pheidole* sp.	Hinton 1951
Brephidium exilis	3**	*Conomyrma insana*	Fernández Haeger 1988
B. isophthalma	3**	*Tapinoma sessile*	Harvey & Longino 1989
Everes amyntula	2**	*Formica obscuripes*	Ballmer & Pratt 1988
		F. (*fusca* gr.)	
Cupido minimus	2*	*Lasius alienus*	Malicky 1969b, Baylis
		L. niger	& Kitching 1988,
		Formica fusca	Fiedler, pers. observ.
		F. rufibarbis	
		Plagiolepis vindobonensis	
		Myrmica rubra	
C. lorquinii	3*	*Tapinoma nigerrimum*	Munguira & Martín 1989,
		Plagiolepis pygmaea	Munguira, pers. comm.
C. osiris	3**	*Lasius alienus*	Malicky 1969b, SBN 1987
Pithecops fulgens	3*(*)	*Camponotus (Myrmanblys)* sp.	Ejima et al. 1978
		C. japonicus ?	
		Paratrechina flavipes ?	
Azanus ubaldus	3**	*Camponotus* sp.	Hinton 1951
		Prenolepis sp.	
A. natalensis	3**	*Cataulacus donisthorpei*	Hinton 1951
		Engramma ilgi	
Celastrina argiolus	2**	*Myrmica* sp.	Malicky 1969b, Harvey &
		Crematogaster lineolatus	Webb 1980, Kitching
		Camponotus japonicus	& Luke 1985, Emmet &
		C. nearcticus	Heath 1990
		Formica subsericea	
		F. truncorum	
		Lasius niger	
		L. alienus	
		L. fuliginosus	
Glaucopsyche lygdamus	3**	*Myrmica brevinodis*	Tilden 1947,
		Tapinoma sessile	Harvey & Webb 1980,
		Formica obscuripes	Pierce & Mead 1981,
		F. lasioides	Ballmer & Pratt in press
		F. subsericea	
		F. fusca	
		F. altipetens	
		F. puberula	
		F. comptula	
		F. neoclara	
G. piasus	3**	*Tapinoma sessile*	Newcomer 1912,
		Conomyrma sp.	Ballmer & Pratt 1988
		Prenolepis imparis	
		Formica pilicornis	

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Glaucopsyche alexis	3**	*Myrmica scabrinodis*	Kontuniemi 1945,
		Crematogaster auberti	Malicky 1969b,
		Tapinoma erraticum	Martín Cano 1981, SBN 1987
		Formica cinerea	
		F. pratensis	
		F. nemoralis	
		F. fusca	
		F. subrufa	
		Camponotus aethiops	
		C. maxiliensis	
		Lasius alienus	
G. melanops	3**	*Camponotus foreli*	Malicky 1969b,
		C. cruentatus	Martín Cano 1981
		C. micans	
		C. sylvaticus	
Maculinea arion	4*	*Myrmica sabuleti*	Thomas et. al. 1989
		M. scabrinodis	
M. arionides	4(*)	*Myrmica* sp.	Iwase 1953
M. teleius	4*	*Myrmica scabrinodis*	Thomas et al. 1989
		M. rubra	
		M. vandeli	
		M. sabuleti	
M. nausithous	4*	*Myrmica rubra*	Thomas et al. 1989
		M. scabrinodis	
M. alcon	4*	*Myrmica ruginodis*	Thomas et al. 1989
		M. rubra	
		M. scabrinodis	Liebig 1989 (lab.)
M. rebeli	4*	*Myrmica schencki*	Thomas et al. 1989,
		M. sabuleti	Jutzeler 1989b
		M. scabrinodis	
		M. sulcinodis	
Iolana iolas	2*	*Tapinoma erraticum*	Warnecke 1932/33,
Pseudophilotes baton	2**	*Myrmica scabrinodis*	Malicky 1969b, Blab &
		Lasius alienus	Kudrna 1982
Euphilotes enoptes	3**	*Crematogaster mormonum*	Opler 1968, Shields 1973,
		Tapinoma sessile	Ballmer & Pratt in press
		Iridomyrmex humilis?	
		Formica neogagates	
Eu. rita	3**	*Dorymyrmex pyramicus*	Shields 1973,
		Camponotus nearcticus	Ballmer & Pratt in press
		C. essigi	
		Myrmecocystus kennedyi	
Eu. battoides	3**	*Tapinoma sessile*	Shields 1973,
		Iridomyrmex humilis	Ballmer & Pratt in press
		Formica (*fusca*-gr.)	
		F. subsericea	
		Lasius pallitarsus	
Eu. bernardino	3**	*Iridomyrmex humilis*	Shields 1973
Philotes sonorensis	3**	*Crematogaster mormonum*	Shields 1973,
		Tapinoma sessile	Ballmer & Pratt in press
		Formica obtusipilosa	

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Scolitantides orion	3**	*Tapinoma erraticum* *Camponotus aethiops* *C. ligniperda* *C. vagus*	Malicky 1969b, Sanetra, pers. comm.
Euchrysops cnejus	3**	*Crematogaster* sp. *Iridomyrmex* sp. *Camponotus rubripes* *C. compressus* *Polyrhachis dives* *P. ammon*	Viehmeyer 1910a, Hinton 1951, Common & Waterhouse 1981
Eu. malathana	3**	*Monomorium* sp. *Pheidole rotundata* (lab) *Camponotus rubripes*	Farquharson 1922, Hinton 1951
Eu. dolorosa	2**	*Camponotus niveosetosus* (lab)	Henning 1983b
Eu. subdita crawshayinus	3**	*Monomorium minutum*	Jackson 1937
Lepidochrysops patricia	4*	*Camponotus maculatus*	Cottrell 1984
L. oreas	4*	*Camponotus niveosetosus*	Cottrell 1984
L. trimeni	4*	*Camponotus maculatus* *Plagiolepis* sp. ??	Henning 1983b
L. ignota	4*	*Camponotus niveosetosus*	Henning 1983b
L. quassi	4*	*Camponotus maculatus*	Farquharson 1922
L. variabilis	4*	*Camponotus niveosetosus*	Cottrell 1984
L. robertsoni	4*	*Camponotus niveosetosus*	Cottrell 1984
L. methymna	4*	*Camponotus maculatus*	Cottrell 1984
L. longifalces	4*	*Camponotus maculatus*	Cottrell 1984
Oboronia punctatus	4(*)	*Pheidole* sp.	Stempffer 1967
Chilades pandava	3**	*Monomorium speculare* *Crematogaster* sp. *Prenolepis longicornis*	Hinton 1951
Ch. lajus	2/3**	*Camponotus rubripes*	Hinton 1951
Ch. trochylus	3**	*Pheidole quadrispinosa* *Iridomyrmex* sp. *Prenolepis* sp.	Hinton 1951, Common & Waterhouse 1981
Ch. parrhasius	3**	*Camponotus sericeus*	Larsen 1984
Ch. galba	3(**)	*Monomorium gracillimum*	Parker 1983
Plebejus argus	3/4**	*Lasius niger* *L. alienus* *Formica cinerea* ??	Kitching & Luke 1985, C. Thomas 1985, Mendel & Parsons 1987, Jutzeler 1989e, Ravenscroft 1990
P. (Plebejides) martini	3**	*Crematogaster* sp.	Rojo de la Paz, pers. comm.
P. (P.) hespericus	3**	*Crematogaster auberti* *Formica subrufa* *F. cinerea* *Plagiolepis pygmaea* *P. schmitzi* *Camponotus cruentatus* *C. foreli* *C. sylvaticus*	Munguira & Martín 1989a, Munguira, pers. comm.

__Table__ __19__ *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Pleb. (Plebejides) trappi	3**	*Formica lugubris*	SBN 1987, Schurian &
		F. lemani	Jutzeler, pers. comm.
P. (P.) sephirus	3**	*Tetramorium (caespitum* gr.)	Bálint & Kertész 1990,
		Formica pratensis	own observ.
		Camponotus aethiops	
		Lasius (alienus gr.)	
P. (Lycaeides) idas	3/4**	*Formica cinerea*	Malicky 1961 & 1969b,
		F. selysi	SBN 1987,
		F. exsecta	Jutzeler 1989d & 1990b
		F. lemani	
		F. pressilabris	
		F. lugubris	
		F. fusca ?	
		F. rufa & *F. nigricans:* attack	
P. (L.) melissa	3**	*Formica neogagates*	Ballmer & Pratt 1988
P. (L.) argyrognomon	3**	*Myrmica scabrinodis*	Malicky 1969b, Blab &
		M. sabuleti	Kudrna 1982
		Lasius alienus	
		L. niger	
P. (Icaricia) icarioides	3**	*Tapinoma sessile*	Downey 1962
		Formica integra	
		F. neogagates	
		F. fusca	
		F. integroides	
		F. oreas comptula	
		F. perspilosa	
		F. lasioides	
		Lasius neoniger	
		Dorymyrmex pyramicus	
		Solenopsis molesta ??	
P. (I.) acmon	3**	*Crematogaster coarctata*	Opler 1968, Ballmer
		Iridomyrmex humilis	& Pratt in press
		Formica pilicornis	
P. (I.) lupini	3**	*Formica pilicornis*	Ballmer & Pratt 1988
P. (I.) shasta	3**	*Formica fusca*	Emmel & Shields 1980,
		F. neogagtes	Ballmer & Pratt 1988
		F. oreas	
		F. densiventris	
P. (Plebulina) emigdionis	3**	*Formica pilicornis*	Ballmer & Pratt 1988
Polyommatus (Aricia) agestis	3**	*Myrmica sabuleti*	Jarvis 1958/59, Kitching
		Lasius alienus	& Luke 1985, Emmet & Heath
		L. flavus	1990, Schurian, pers. comm.
P. (A.) artaxerxes	3**	*Lasius* sp.	Malicky 1969b, SBN 1987
P. (A.) morronensis	3**	*Crematogaster auberti*	Munguira & Martín 1988
		Tapinoma erraticum	
		T. nigerrimum	
		Lasius niger	
P. (A.) eumedon	3**	*Myrmica* sp.	Malicky 1969b, Weidemann
			1986, SBN 1987

Table 19 (continued)

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Polyommatus (Agrodiaetus) damon	3**	*Lasius niger*	Warnecke 1932/33, SBN 1987
		Formica pratensis	Malicky 1969b
P. (A.) thersites	3**	*Myrmica scabrinodis*	Rehfous 1954,
		Tapinoma erraticum	Malicky 1969b,
		Lasius alienus	Schurian, pers. comm.
P. (A.) semiargus	3**	*Lasius* sp.	Weidemann 1986
P. (Lysandra) coridon	3**	*Myrmica scabrinodis*	Malicky 1969b, Kitching
		M. sabuleti	& Luke 1985, Fiedler 1987b,
		M. schencki	Fiedler & Rosciszewski 1990
		Tetramorium caespitum	
		Lasius niger	
		L. alienus	
		L. flavus	
		L. fuliginosus ??	
		Plagiolepis vindobonensis	
		Formica rufa	
P. (L.) hispana	3**	*Crematogaster sordidula*	Maschwitz et al. 1975,
		Plagiolepis pygmaea	Schurian, pers. comm.
P. (L.) bellargus	3**	*Myrmica sabuleti*	Warnecke 1932/33,
		M. scabrinodis	Malicky 1969b, Blab &
		Tapinoma erraticum	Kudrna 1982, Kitching &
		Lasius alienus	Luke 1985, Jutzeler 1989c
		L. niger	
		L. flavus	
		Plagiolepis pygmaea	
P. (L.) punctifera	3**	*Monomorium salomonis*	Schurian & Thomas 1985
		Crematogaster scutellaris	
P. (L.) amandus	3**	*Lasius niger*	Hornemann, pers. comm.
P. (L.) escheri	3**	*Myrmica specioides*	SBN 1987, Fiedler, pers. obs.
		Formica cinerea	
P. (L.) dorylas	3**	*Myrmica scabrinodis*	Rehfous 1954, Weidemann
		Lasius alienus	1986, SBN 1987
		Formica cinerea	
P. (L.) golgus	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (L.) nivescens	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (Meleageria) daphnis	3**	*Tapinoma erraticum*	Schurian, pers. comm.,
		Formica pratensis	Fiedler, pers. obs.
		Lasius alienus	
P. (Polyommatus) icarus	2/3**	*Myrmica sabuleti*	Malicky 1969b,
		Lasius alienus	Martín Cano 1984,
		L. niger	Kitching & Luke 1985,
		L. flavus (lab)	SBN 1987, Jutzeler 1989d,
		Formica subrufa	Emmet & Heath 1990
		F. cinerea ?	
		Plagiolepis pygmaea	
P. (P.) eros	2/3**	*Myrmica gallienii*	Jutzeler 1989a
		Formica lemani	
Hemiargus ceraunus	3**	*Forelius pruinosus*	Ballmer & Pratt in press

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